

# Revision of the Gastropteridae (Opisthobranchia: Cephalaspidea) with Descriptions of a New Genus and Six New Species

by

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*Abstract.* Fifteen species of Gastropteridae are here recorded from the tropical Pacific and Atlantic oceans. Three of these are described as new species of *Siphopteron* gen. nov. and three as species of *Gastropteron*. *Sagaminopteron psychedelicum* Carlson & Hoff, 1974, and *G. bicornutum* Baba & Tokioka, 1965, are recorded from Papua New Guinea and their morphology is described. *Siphopteron pohnpei* (Hoff & Carlson, 1983) is recorded from the Hawaiian Islands. These constitute the first records of these species since their original descriptions. *Siphopteron brunneomarginatum* (Carlson & Hoff, 1974), known from Guam and Enewetak, is also recorded from Papua New Guinea. The morphology of an additional species from Easter Island is described. This probably represents an additional undescribed species, but inadequate material prevents its description here.

Additional aspects of the morphology of *Sagaminopteron bilealbum* Carlson & Hoff, 1973, *Sagaminopteron nigropunctatum* Carlson & Hoff, 1973, *Siphopteron flavum* (Tokioka & Baba, 1964) and *Siphopteron citrinum* (Carlson & Hoff, 1974) are described. The morphology of all species is described in order to present a more coherent picture of morphological variability within the family. This variability permits a phylogenetic analysis of the Gastropteridae and requires the description of *Siphopteron*.

## INTRODUCTION

The Gastropteridae had received little attention since the early works of VAYSSIÈRE (1885) and BERGH (1893). TOKIOKA & BABA (1964), BABA & TOKIOKA (1965), and BABA (1970) rekindled interest and activity with the description of several species of Gastropteridae and a new genus from Japanese material. MINICHEV (1967) described an additional genus and species from China. CARLSON & HOFF (1973, 1974) and HOFF & CARLSON (1983) described several new taxa from the tropical western Pacific. GOSLINER & ARMES (1984), GOSLINER (1984, 1988a), and GOSLINER & WILLIAMS (1988) have added several other new taxa from various portions of the world's oceans.

On recent collecting trips to the Caribbean coast of Mexico, the Hawaiian Islands and Papua New Guinea, Michael Ghiselin and I have collected specimens of several species of Gastropteridae. These all constitute new records or undescribed species. Specimens of four previously described gastropterids were provided by Clay Carlson, Patty Jo Hoff, and Pauline Fiene. Additional specimens have been provided from collections made at Turks and Caicos islands in the Caribbean by Jeff Hamann, from Japan by the Royal Swedish Museum, and from Easter Island by Louis de Salvo. As little is known about the internal morphology of most members of the Gastropteridae, it is imperative to provide complete descriptions for all species, in order that comparative morphological studies can be employed to suggest phylogenetic relationships within the family.

## DESCRIPTIONS

*Sagaminopteron psychedelicum* Carlson & Hoff, 1974

(Figures 1A, 2, 3)

*Sagaminopteron psychedelicum* CARLSON & HOFF, 1974:354, text figs. 7-10, 12a, 13e, fig. 4).

**Distribution:** This species is known only from Guam and Pagan, Marianas Islands (CARLSON & HOFF, 1974) and Papua New Guinea (present study). Dr. Maurice Jay (pers. comm.) has collected this species from Reunion Island, in the western Indian Ocean.

**Material:** One specimen, California Academy of Sciences, San Francisco, CASIZ 066549, dissected, harbor wall, Madang, Papua New Guinea, 22 m depth, 1 October 1986, T. M. Gosliner. One specimen, CASIZ 066550, dissected, Cement Mixer Reef, Madang, Papua New Guinea, 2 m depth, 20 October 1987, T. M. Gosliner. One specimen, CASIZ 066551, off Madang Resort Hotel, Madang, Papua New Guinea, 3 m depth, 1 February 1988, T. M. Gosliner. One specimen, CASIZ 066552, dissected, The Quarry, 30 km N of Madang, Papua New Guinea, 3 m depth, 12 February 1988, T. M. Gosliner. One specimen, CASIZ 066553, dissected, The Quarry, 30 km N of Madang, Papua New Guinea, 6 m depth, 14 February 1988, G. Williamson.

**Natural history:** Specimens of *Sagaminopteron psychedelicum* have been collected from shallow to relatively deep (22 m) rocky reefs. Animals were observed to swim in the laboratory. Though other members of the genus are known to feed on sponges (CARLSON & HOFF, 1973; R. C. Willian, pers. comm.), specimens of *S. psychedelicum* have not been observed in association with any prey.

**External morphology:** The living animals (Figure 1A) were 3.5-12 mm in length. Their color is vivid and complex. The ground color of the head shield, parapodia, and visceral hump is pale green. A series of off-white and olive-green patches are present over the surface of the body. Each patch is encircled by a narrow well-defined line of black. The margins of the parapodia consist of a narrow inner black line followed by broad milky white band. The tip of the cream flagellum and anterior corners of the head shield are pale lavender. The apex of the siphon is orange. The gills are translucent white with opaque milky white flecks scattered over their surfaces.

The head shield is roughly triangular in shape, broadest anteriorly. The anterior ends are extended into two short, roughly triangular tentacles. The posterior end of the head shield is involuted into a siphon with a medial crest that terminates in a distinctly elevated apical papilla.

The parapodia are elongate and convoluted along their outer margin. They are relatively low, not covering much of the visceral hump, when the animal is actively crawling. The parapodia extend well beyond the visceral hump to the posterior end of the foot. The visceral hump is elongate and ovoid, comprising approximately two-thirds of the body length. On the posterior end of the visceral hump, just to the right of the median line, is a short conical flagellum. Several small ovoid tubercles are present on the posterior portion of the visceral hump. The ctenidium is tripinnate consisting of four distinct gills. Each gill is divided into approximately eight pinnae with approximately four pinnules per pinna. The foot is broad, not distinctly separate from the parapodia. A posterior pedal gland is visible on the ventral surface of the foot.

**Digestive system:** The buccal mass (Figure 2A) is short and highly muscular. The esophagus joins the buccal mass on the right side of the body. At this juncture is a pair of large, straplike, ventrally directed salivary glands. Within the buccal mass is a pair of jaws bearing several rows of rodlets (Figure 3A). Also contained within the buccal mass is the radula. Its formula in the largest specimen (CASIZ 066550) was  $33 \times 9-10 \cdot 1 \cdot 0 \cdot 1 \cdot 9-10$ . The inner lateral teeth (Figure 3B, C) are broad with an elongate, pointed cusp. The inner margin of the tooth bears two large triangular denticles. The second lateral teeth are broad with a single blunt denticle. The remaining outer laterals (Figure 3D) are curved with a single cusp and no other denticles. They become successively smaller towards the outer margin of the radula.

**Central nervous system:** The arrangement of ganglia (Figure 2B) is euryneurous, with a short visceral loop. The cerebral ganglia are large and appressed to each other, without a distinct commissure. The pedal ganglia are as large as the cerebrals and are separated by an elongate commissure, which is ventral to the buccal mass. Posterior to the left cerebral ganglion are the left pleural, subintestinal, and visceral ganglia. From the visceral ganglion emanate the visceral loop and an additional visceral nerve. The visceral loop joins the posterior end of the supra-intestinal ganglion on the right side of the head. An os-

Figure 1

Living animals. A. *Sagaminopteron psychedelicum* Carlson & Hoff, 1974. B. *Siphopteron brunneomarginatum* (Carlson & Hoff, 1974). C. *Siphopteron nigromarginatum* Gosliner, sp. nov. D. *Siphopteron pohrpei* (Hoff & Carlson, 1983). E. *Siphopteron quadrispinosum* Gosliner, sp. nov. F. *Siphopteron tigrinum* Gosliner, sp. nov. G. *Gastropteron bicornutum* Baba & Tokioka, 1965. H. *Gastropteron hamanni* Gosliner, sp. nov. I. *Gastropteron chacmol* Gosliner, sp. nov.





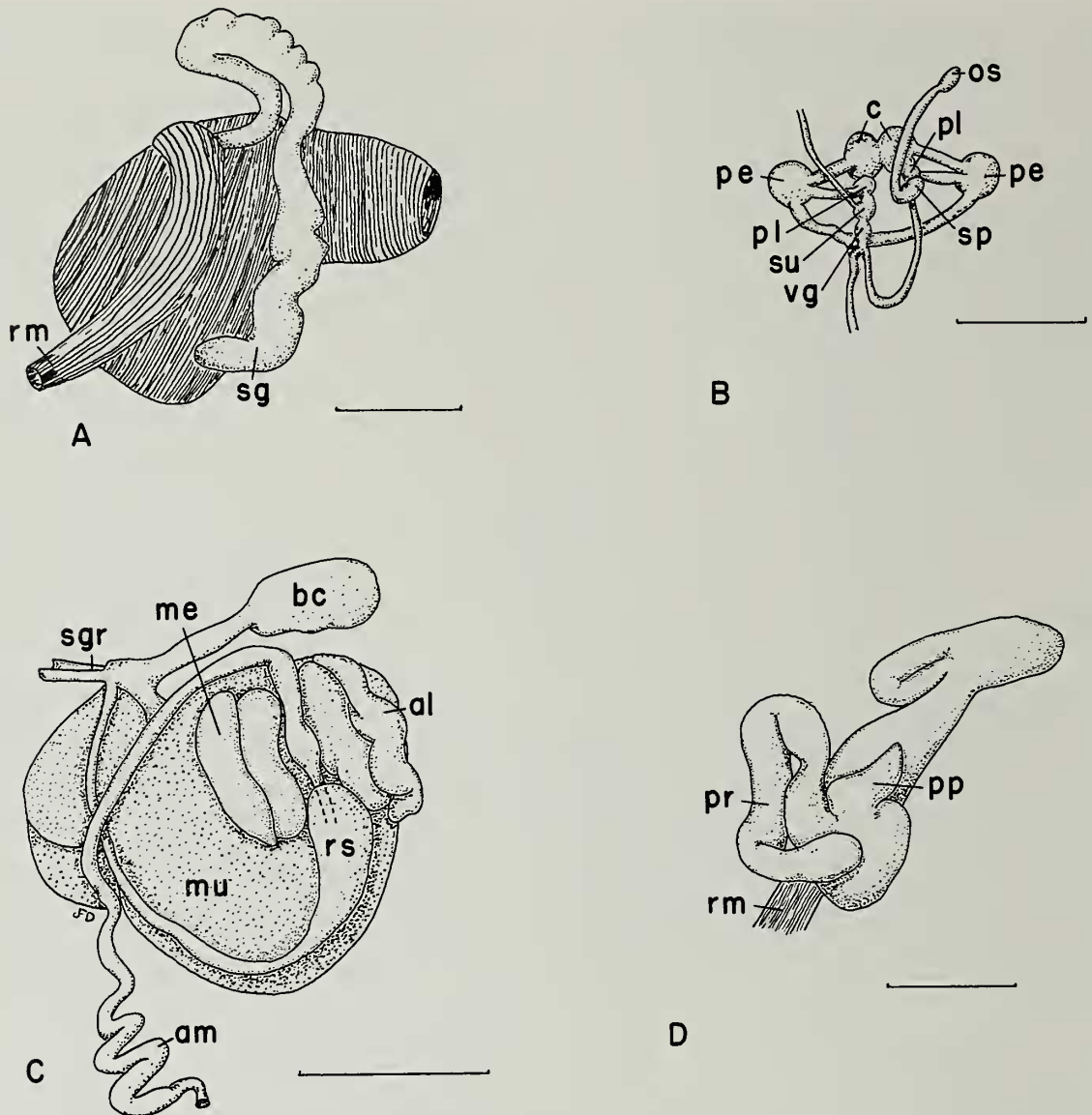


Figure 2

*Sagaminopteron psychedelicum* Carlson & Hoff, 1974. A. Buccal mass, scale = 0.5 mm. Key: rm, retractor muscle; sg, salivary gland. B. Central nervous system, scale = 1.0 mm. Key: c, cerebral ganglion; os, osphradial ganglion; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Reproductive system, scale = 1.0 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane papilla; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. D. Penis, scale = 0.5 mm. Key: pp, penial papilla; pr, prostate; rm, retractor muscle.

phradial nerve joins the supraintestinal and osphradial ganglia. The supraintestinal ganglion joins the posterior end of the right pleural ganglion.

**Reproductive system:** The detailed anatomy of the posterior reproductive system was examined in CASIZ 066553 (Figure 2C). Other specimens were immature or poorly preserved. One specimen (CASIZ 066550) was parasitized

by a copepod, and the reproductive organs were poorly developed. The narrow, convoluted ampulla straightens into the hermaphroditic duct which curves around the surface of the large, lobate mucous gland. On the outer side of the gland mass, the hermaphroditic duct passes between the smaller, convoluted albumen and membrane glands. Near this point, the pyriform receptaculum seminis joins the hermaphroditic duct. The duct continues to the



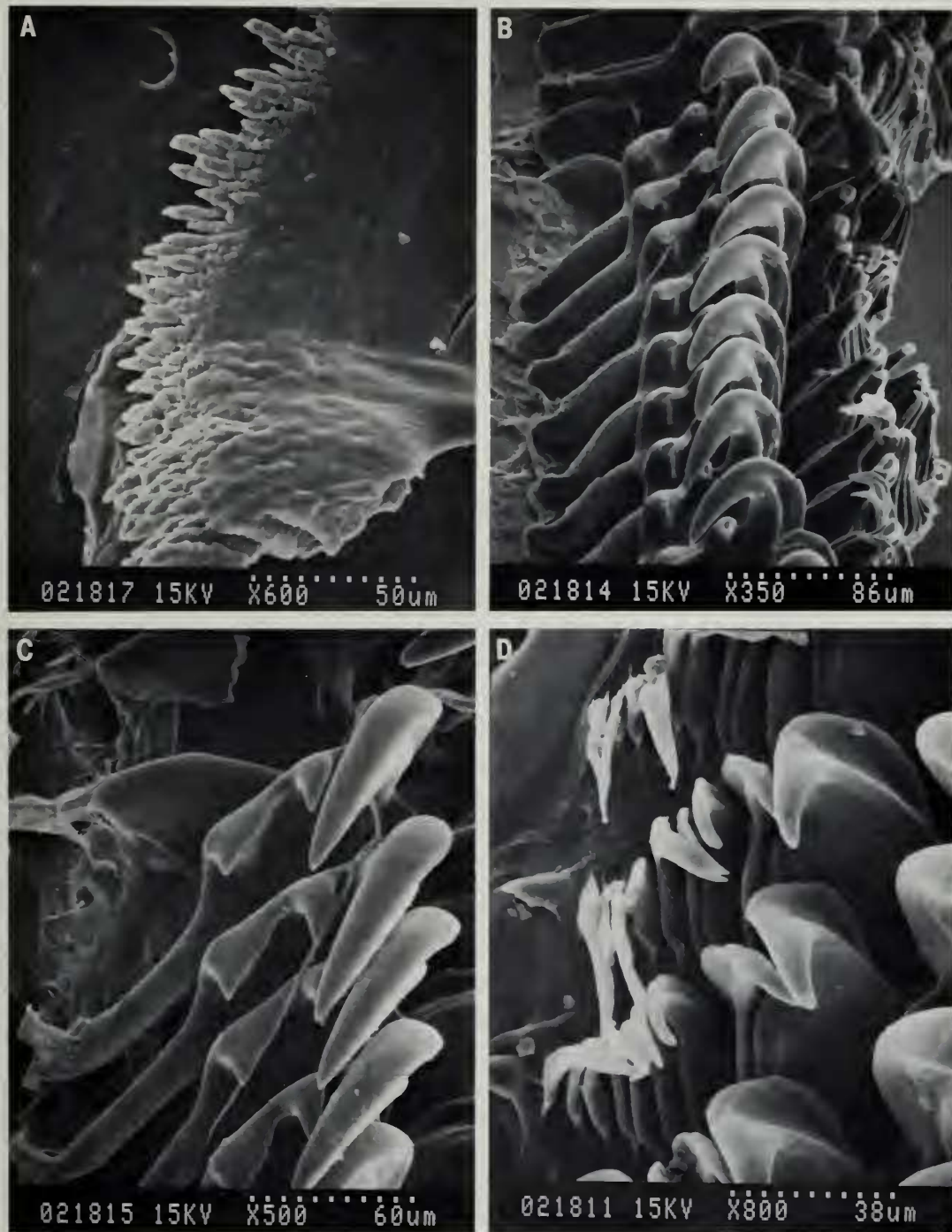


Figure 3

*Sagaminopteron psychedelicum* Carlson & Hoff, 1974. Scanning electron micrographs. A. Jaw elements. B. Half-row of radular teeth. C. Inner lateral teeth. D. Outer lateral teeth.

gonopore where it unites with the female glands and the short duct of the bursa copulatrix. From the gonopore, a ciliated sperm groove conducts spermatozoa to the penis, situated on the right side of the head.

The structure of the penis (Figure 2D) was determined in detail. The prostate is elongate and recurved. At its junction with the penial sac is a large retractor muscle. Within the penial sac is a simple, conical, unarmed papilla.

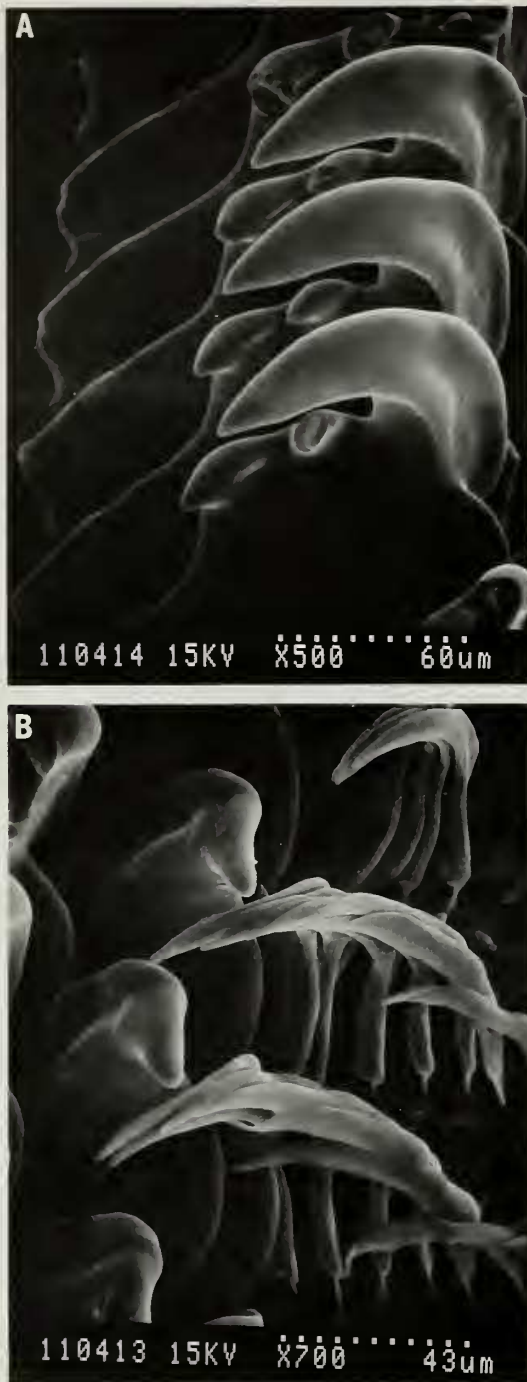


Figure 4

*Sagaminopteron bilealbum* Carlson & Hoff, 1973. Scanning electron micrographs. A. Inner lateral teeth. B. Outer lateral teeth.

Near the junction of the penis with the sperm groove is an expanded portion of the penis that may function as a spermatic bulb or for short-term sperm storage.

**Discussion:** The external morphology and coloration of

the present material closely match those of the original description of *Sagaminopteron psychedelicum* Carlson & Hoff, 1974. The radula of the larger specimen examined here had slightly more rows of teeth, but otherwise corresponded to the original description.

*Sagaminopteron bilealbum* Carlson & Hoff, 1973

(Figures 4, 5)

*Sagaminopteron bilealbum* CARLSON & HOFF, 1973:145, figs. 4-8, pl. 9, figs. 3, 4.

**Material:** Four specimens, California Academy of Sciences, San Francisco, CASIZ 066554, 066555, reef flat, Bile Bay, Merizo, Guam, 12 October 1988, C. H. Carlson and P. J. Hoff.

**Distribution:** This species is known only from Guam.

**External morphology:** The animals ranged from 3.5 to 12 mm in length. In aspects of their external morphology, they are identical to the original description.

**Digestive system:** The buccal mass is large and muscular. A pair of long, straplike salivary glands is present on either side of the esophagus. Near the anterior end of the buccal mass is the thin, cuticular jaw, which has longitudinal thickenings, but is devoid of rodlets. The radular formula in the 12-mm animal (CASIZ 066555) is  $37 \times 8 \cdot 1 \cdot 0 \cdot 1 \cdot 8$ . The inner lateral teeth (Figure 4A) have an elongate curved cusp with two large denticles on the inner face of the teeth. The second lateral teeth are broad with a single short cusp. The remaining outer lateral teeth are smaller than the inner ones and lack denticles other than the main cusp (Figure 4B). The teeth become increasingly narrow towards the outer edge of the radula.

**Central nervous system:** The arrangement of ganglia (Figure 5A) is similar to that observed in *Sagaminopteron psychedelicum*. The large cerebral ganglia are appressed to each other, without a distinct commissure. There are large, anteriorly directed ganglionic masses anterior to the cerebral ganglia. The pedal ganglia are approximately the same size as the cerebrals and are situated lateroventrally to them. The pedals are connected to each other by an elongate commissure and are joined to the cerebral and pleural ganglia by elongate connectives. Immediately posterior to the left pleural ganglion are the subintestinal and visceral ganglia. The visceral loop extends posteriorly from the visceral ganglion, recurves anteriorly, and joins the posterior end of the suprainintestinal ganglion. The suprainintestinal joins anteriorly with the right pleural ganglion.

**Reproductive system:** The reproductive system is monaulic (Figure 5B). The convoluted ampulla narrows into the hermaphroditic postampullary duct and curves around the perimeter of the large, ovoid mucous gland. It passes between the small albumen and membrane glands. In this region a pyriform receptaculum seminis joins the her-

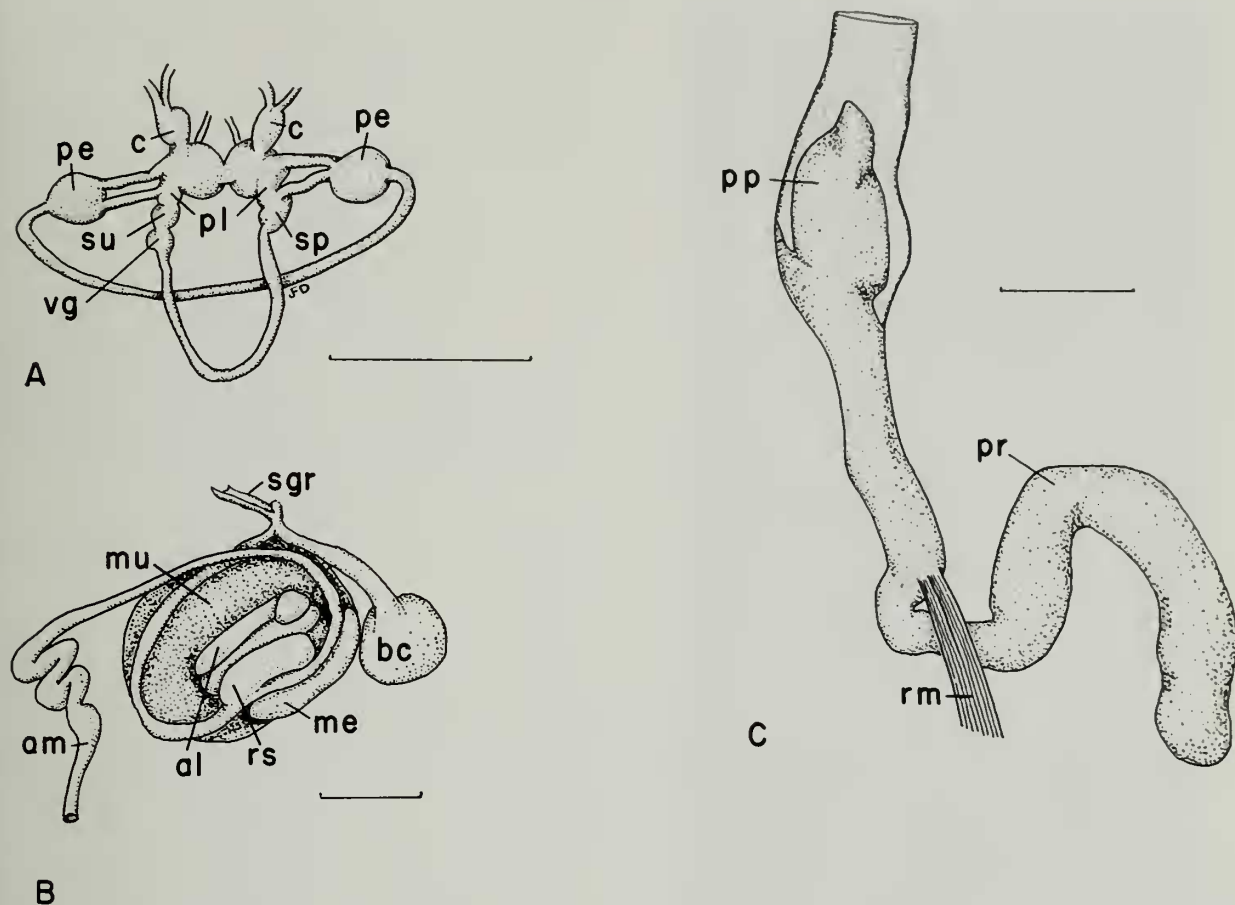


Figure 5

*Sagaminopteron bilealbum* Carlson & Hoff, 1973. A. Central nervous system, scale = 1.0 mm. Key: c, cerebral ganglion; pe, pedal ganglia; pl, pleural ganglia; sp, subintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. B. Reproductive system, scale = 1.0 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. C. Penis, scale = 0.25 mm. Key: pp, penial papilla; pr, prostate; rm, retractor muscle.

maphroditic duct. At this point the hermaphroditic duct widens somewhat and recurves to the hermaphroditic gonopore. The spherical, thin-walled bursa copulatrix joins the gonopore by means of a thin, straight duct. From the gonopore the ciliated sperm groove conducts endogenous sperm to the penis, situated on the right side of the head.

The penis (Figure 5C) has an elongate, slightly convoluted prostate. A retractor muscle is attached near the middle of the prostate. The penial papilla is simple, unarmed, and anteriorly rounded.

**Discussion:** This species is most similar to its congener *Sagaminopteron nigropunctatum* Carlson & Hoff, 1973. Though they are sympatric on different species of the same genus of sponges (CARLSON & HOFF, 1973), *S. bilealbum* and *S. nigropunctatum* have several internal and external morphological differences. In *S. nigropunctatum* the parapodia are more reduced and this species is rarely observed

swimming. This species also bears black spots and orange pigment on the rhinophoral crest and flagellum that are absent in *S. bilealbum*. Internally, the shell is proportionately larger in *S. nigropunctatum* than in *S. bilealbum*. In *S. nigropunctatum* the prostate is more highly convoluted and the penial papilla is more lobate than in *S. bilealbum*.

*Sagaminopteron nigropunctatum* Carlson & Hoff, 1973

(Figures 6, 7)

*Sagaminopteron nigropunctatum* CARLSON & HOFF, 1973:141, figs. 1-3, 7, 8, pl. 9, figs. 1, 2.

**Distribution:** This species is known only from the type locality on Guam.

**Material:** Four specimens, California Academy of Sciences, San Francisco, CASIZ 066556, 066557, Bile Bay,





Figure 6

*Sagaminopteron nigropunctatum* Carlson & Hoff, 1973. Scanning electron micrographs. A. Inner lateral teeth. B. Outer lateral teeth.

Merizo, Guam, 1–3 m depth, 12 October 1988, C. H. Carlson and P. J. Hoff.

**External morphology:** The living animals were 3–10 mm long. In all aspects of their external morphology, they are identical to material described by CARLSON & HOFF (1973).

**Digestive system:** The buccal mass is large and muscular. A chitinous lining is devoid of distinct jaw platelets. The radular formula in the 10-mm specimen (CASIZ 066557) was  $32 \times 9 \cdot 1 \cdot 0 \cdot 1 \cdot 9$ . The inner lateral teeth (Figure 6A) are broad with a large curved cusp and two smaller, triangular inner denticles. The second lateral tooth is smaller than the inner lateral, with only a single short cusp. The succeeding outer laterals (Figure 6B) are proportionately smaller and thinner than the second lateral, and become increasingly smaller towards the outer margin of the radula.

**Central nervous system:** The arrangement of ganglia is identical to that of *Sagaminopteron bilealbum*.

**Reproductive system:** The arrangement of organs (Figure 7A) is monaulic, and similar to the two preceding species. A large convoluted ampulla narrows into a post-ampullary hermaphroditic duct. The hermaphroditic duct curves around the margin of the large, lobate mucous gland and passes next to the smaller albumen and membrane glands. Here it joins the pyriform receptaculum seminis, and continues towards the hermaphroditic gonopore, where it joins the duct of the spherical bursa copulatrix, at the common gonopore.

The ciliated sperm groove terminates on the right side of the head, where the simple penis is situated. The penis (Figure 7B) has a large, convoluted prostate, which ends in a simple, lobed penial papilla. A retractor muscle is situated near the juncture of the penial papilla and prostate.

#### *Siphopteron* Gosliner, gen. nov.

**Type species:** *Siphopteron tigrinum* Gosliner, sp. nov., by original designation.

**Etymology:** *Siphopteron* is named for the prominent siphonal crest and parapodial “wings” that characterize members of the genus.

**Diagnosis:** Gastropteridae with or without an internal shell. Head shield small, roughly triangular, with well-developed siphonal crest, bearing a prominent dorsal ridge. Parapodia short or long and overlapping. Visceral hump roughly ovoid. Flagellum present or absent. When present, single on right side or terminal. Gill simple with many or few pinnae. Foot triangular posteriorly, with large pedal gland. Jaw platelets present or absent. Radula with 2–6 outer lateral teeth per side. Inner laterals large, with or without denticles. Cerebral commissure short or absent. Subintestinal and visceral ganglia distinct or fused. Penis

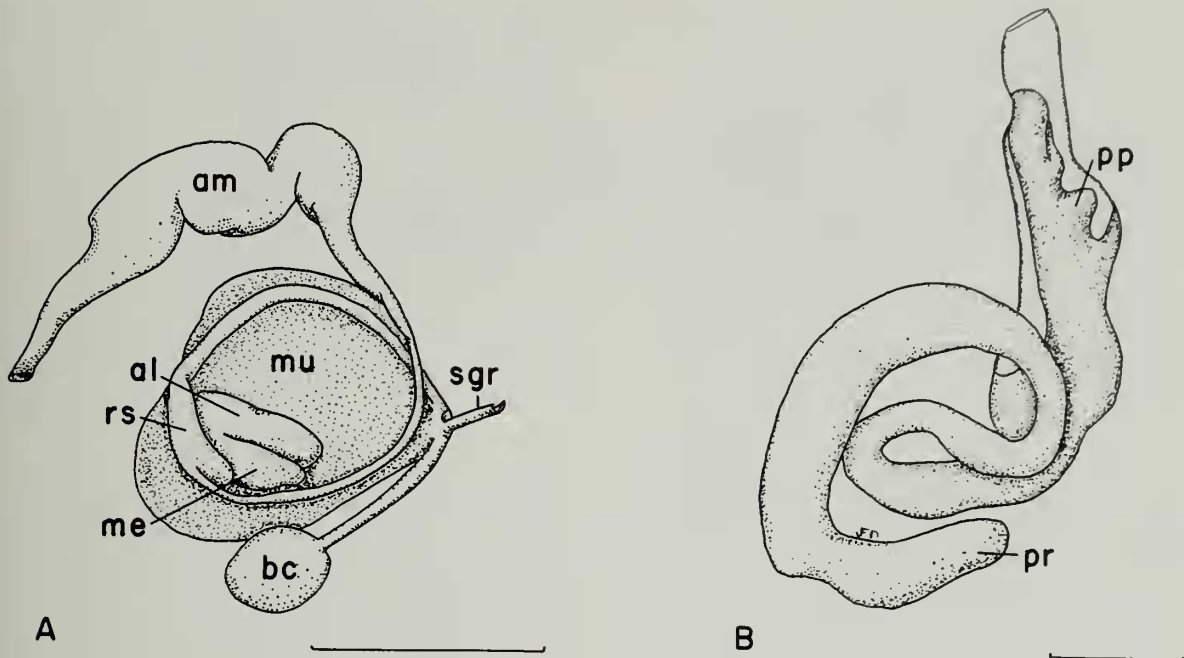


Figure 7

*Sagaminopteron nigropunctatum* Carlson & Hoff, 1973. A. Reproductive system, scale = 1.0 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. B. Penis, scale = 0.25 mm. Key: pp, penial papilla; pr, prostate.

complex, with spermatid bulb or separate penial duct and bulb, often armed with rows of chitinous spines.

*Siphopteron brunneomarginatum*  
(Carlson & Hoff, 1974)

(Figures 1B, 8, 9)

*Gastropteron brunneomarginatum* CARLSON & HOFF, 1974:  
347, text figs. 1, 2, 12c, 13b, pl. X, fig. 1; KAY &  
JOHNSON, 1987:126.

*Siphopteron brunneomarginatum* (Carlson & Hoff, 1974)  
comb. nov.

**Distribution:** *Siphopteron brunneomarginatum* has been recorded from the type locality, Guam (CARLSON & HOFF, 1974), Enewetak Atoll (KAY & JOHNSON, 1987), and Papua New Guinea (present study).

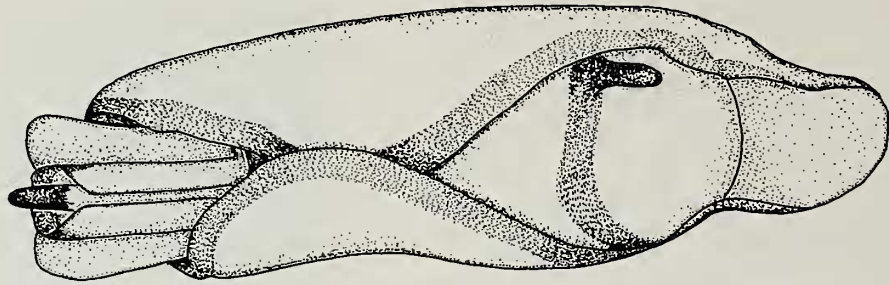
**Material:** One specimen, California Academy of Sciences, San Francisco, CASIZ 064350, dissected, Cement Mixer Reef, Madang, Papua New Guinea, 2 m depth, 22 October 1986, T. M. Gosliner. Two specimens, CASIZ 064352, Barracuda Point, Madang, Papua New Guinea, 10 m depth, 12 October 1986, T. M. Gosliner. One specimen with egg mass, CASIZ 064359, Cement Mixer Reef, Madang Papua New Guinea, 2 m depth, 20 October 1986, T. M. Gosliner. One specimen, CASIZ 066358, Cement Mixer Reef, Madang, Papua New Guinea, 2 m depth, 20

October 1986, T. M. Gosliner. One specimen, CASIZ 066559, The Chimney, Madang, Papua New Guinea, 10 m depth, 30 January 1988, T. M. Gosliner. One specimen CASIZ 066560, dissected, Planet Rock, Madang, Papua New Guinea, 10 m depth, 28 January 1988, T. M. Gosliner. One specimen, CASIZ 066561, The Quarry, N of Madang, Papua New Guinea, 12 m depth, 11 February 1988, T. M. Gosliner.

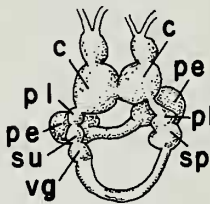
**Natural history:** Specimens of this species have been observed on the underside of coral rubble on shallow-water reefs. This species has not been observed to swim, either in the field or laboratory.

**External morphology:** The living animals (Figure 1B) are 3–5 mm in length. The body is uniformly light greenish yellow with chocolate brown lines extending along the margins of the parapodia to the foot, as a transverse band on the visceral hump, which extends on to the flagellum, when present, and on the apex of the siphon.

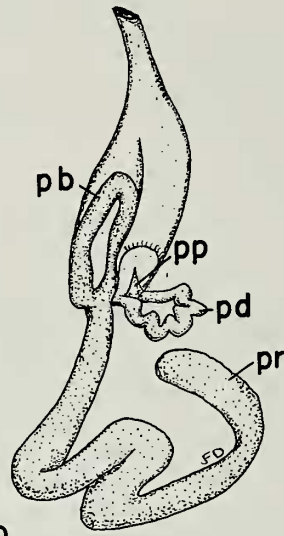
The head shield (Figure 8A) is short and triangular with an involuted siphon at its posterodorsal end. The siphon contains a medial crest whose apex is slightly elevated above the rest of the siphon. The visceral hump is elongate and posteriorly rounded. An elongate, conical flagellum is present on the right side of the visceral hump, in four of the five specimens collected in 1986 and all of the 1988 specimens. It is entirely absent in the fifth 1986



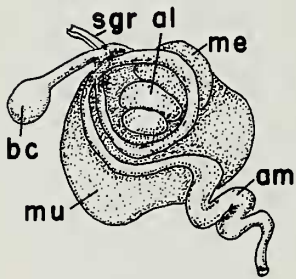
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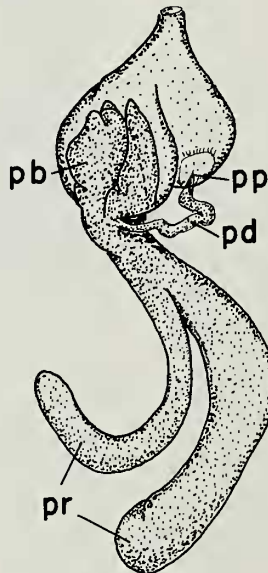
B



D



C



E



specimen. The parapodia are elongate and high. Near the middle of the body the margins of the two parapodia touch or overlap each other. The gill is small and consists of 3 or 4 simple plicae.

**Digestive system:** A large ventral oral gland is present on the ventral side of the muscular buccal mass. An elongate, convoluted salivary gland is present on either side of the junction of the esophagus with the posterior end of the buccal mass. No distinct jaw platelets are present on the chitinous lining within the buccal mass. The radular formula was  $23 \times 3 \cdot 1 \cdot 0 \cdot 1 \cdot 3$  in one specimen observed. The inner lateral teeth (Figure 9A, B) bear 5–7 small, irregular denticles along the inner margin of the elongate central cusp. The outer laterals (Figure 9A) are narrower and lack denticles other than the central cusp.

**Central nervous system:** The arrangement of ganglia is euthyneurous (Figure 8B). The cerebral ganglia are large and appressed to each other, without a distinct commissure. Dorsal to each cerebral ganglion is a slightly smaller concentration of nervous tissue. The eyes are situated at the end of short optic nerves, which emanate from the cerebral ganglia. Ventral to each cerebral ganglion is a slightly smaller pedal ganglion. The pedal ganglia are joined by a short commissure that passes under the ventral surface of the buccal mass. Each pedal ganglion is joined to a cerebral and pleural ganglion by short connectives. Immediately posterior to the left cerebral ganglion is the small left pleural ganglion. Posterior to it are the subintestinal and slightly larger visceral ganglia. From the posterior end of the visceral ganglion, the visceral nerve curves under the esophagus and crop and joins the supraintestinal ganglion on the right side of the body. Immediately anterior to the supraintestinal ganglion is the right pleural ganglion.

**Reproductive system:** The reproductive system is monaulic (Figure 8C). The ampulla is narrow and convoluted for most of its length. The hermaphroditic duct curves around the proximal portion of the female gland mass. No distinct receptaculum seminis was observed in either of the two specimens dissected. The albumen and membrane glands are encircled by a loop of the hermaphroditic duct. The hermaphroditic duct exits at the gonopore, adjacent to the sperm groove and the duct of the spherical, thin-walled bursa copulatrix.

The penis (Figure 8D, E) is complex in structure. Either one or two prostates are present. If two are present, one is thicker than the other. Both protates are elongate and curved or convoluted. At their distal end is a narrow, convoluted duct, which joins the penial papilla in the penial sac. Adjacent to the penial papilla is a larger fleshy papilla, which is entirely devoid of any chitinous spines. A narrow retractor muscle is present on the inner side of the penis at the junction of the prostate with the penial sac.

**Discussion:** The external and radular morphology of *Siphopteron brunneomarginatum* were described by CARLSON & HOFF (1974). Nothing in the present material differs from the original description, with the exception of the variability of the presence or absence of a flagellum in some of the present material.

The penial morphology is similar to several other Indo-Pacific taxa (GOSLINER & WILLIAMS, 1988; present study) in that a distinct narrow duct runs from the junction of the penial sac and prostate to the penial papilla. However, only *Siphopteron brunneomarginatum*, *S. citrinum*, and *S. pohnppei* (Hoff & Carlson, 1983) are known to lack rows of chitinous spines in the penial bulb. The three species differ in their coloration. *Siphopteron brunneomarginatum* is the only one of the three species that possesses dark brown parapodial margins. The other two lack contrasting pigment on the margins.

The denticles on the radular teeth of *Siphopteron pohnppei* are far more prominent than in *S. brunneomarginatum* or *S. citrinum*. Although the three species lack spines on the penial bulb, there are some other differences in the structure of the penis. In *S. brunneomarginatum* and *S. citrinum* the prostate is more elongate than in *S. pohnppei*. More significantly, in *S. brunneomarginatum* the narrow duct that leads to the penial papilla begins at the junction of the prostate and penial bulb, whereas in *S. pohnppei* the duct is connected with the distal end of the penial sac (Figure 14C). The penial duct of *S. citrinum* is much shorter and thicker than that of *S. brunneomarginatum*.

*Siphopteron citrinum* (Carlson & Hoff, 1974)

(Figures 10, 11)

*Gastropteron citrinum* CARLSON & HOFF, 1974:350, text figs. 3, 4, 12d, 13c, pl. 10, fig. 2.

*Siphopteron citrinum* (Carlson & Hoff, 1974) comb. nov.

Figure 8

*Siphopteron brunneomarginatum* (Carlson & Hoff, 1974). A. Living animal, scale = 1.0 mm. B. Central nervous system, scale = 1.0 mm. Key: c, cerebral ganglion; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Reproductive system, scale = 0.25 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; sgr, sperm groove. D. Penis with undivided prostate, scale = 0.5 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla; pr, prostate. E. Penis with bilobed prostate, scale = 0.5 mm. Lettering same as in D.

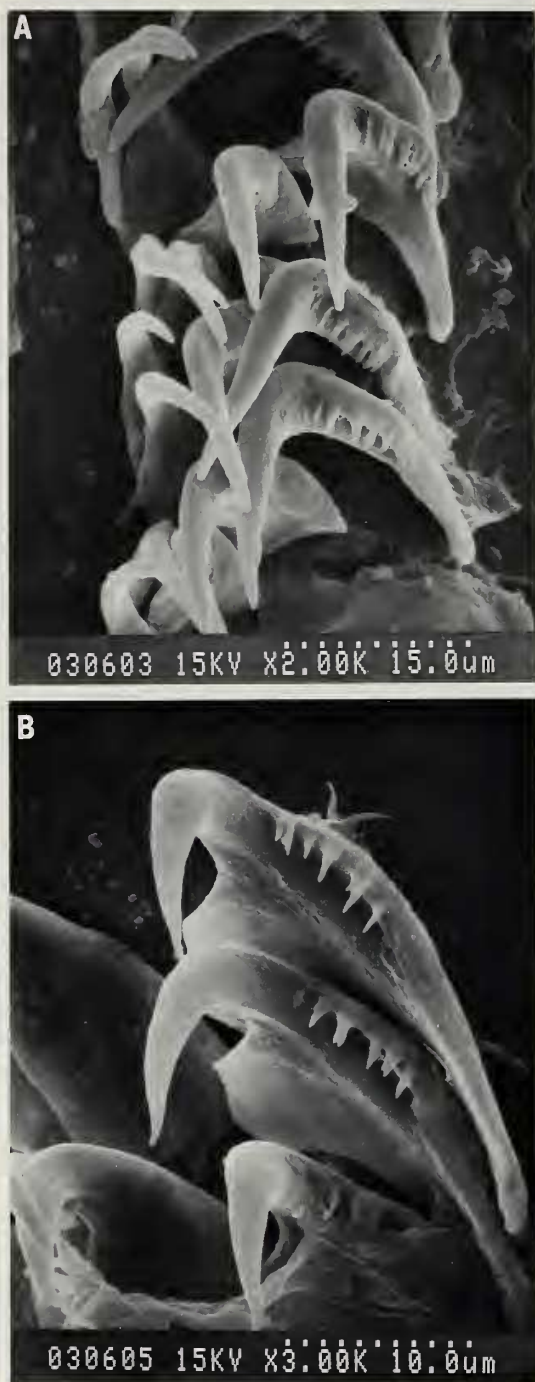


Figure 9

*Siphopteron brunneomarginatum* (Carlson & Hoff, 1974). Scanning electron micrographs A. Half-row of radular teeth. B. Inner lateral teeth.

**Distribution:** This species is known only from the type locality, Guam (CARLSON & HOFF, 1974).

**Material:** Two specimens, California Academy of Sciences, San Francisco, CASIZ 066759, Bile Bay, Merizo, Guam, 11 December 1988, C. H. Carlson and P. J. Hoff.

**External morphology:** The two living animals were 4.0 mm in length. In aspects of their external morphology, they are identical to the original description.

**Digestive system:** The buccal mass is small and muscular. A pair of short, convoluted salivary glands is present on either side of the esophagus. Within the buccal mass is a thin chitinous cuticle, which is devoid of distinct jaw platelets. The radula is situated posteriorly. Its formula in one specimen is  $21 \times 3.1 \cdot 0.1 \cdot 3$ . The inner lateral teeth (Figure 11A) are broad with an elongate, curved primary cusp. A single small triangular denticle is present near the outer margin of the masticatory margin. The outer lateral teeth (Figure 11B) are simple and hook-shaped. They become progressively smaller towards the outer margins.

**Central nervous system:** The arrangement of ganglia (Figure 10A) is euthyneurous, with a short visceral loop. The paired cerebral ganglia are large and spherical. They are closely appressed, without a distinct commissure separating them. A distinct ganglionic mass is present dorsal to either cerebral ganglion. The pedal ganglia are situated ventral to the cerebral ganglia, and are joined to them by short connectives. The pedal ganglia are joined to each other by an elongate connective. Posterior to the left cerebral ganglion is the small left pleural ganglion. It is also joined to the left pedal ganglion by a short connective. Immediately posterior to the left pleural ganglion is the subintestinal ganglion. A short distance behind the subintestinal ganglion is the visceral ganglion. From it extends the visceral loop, which curves to the right and anteriorly. On the right side of the body the visceral loop joins the posterior end of the largely fused suprainestinal and right pleural ganglia.

**Reproductive system:** The arrangement of organs (Figure 10B) is monaulic. The ampulla is thick, with three or four convolutions. It narrows into the hermaphroditic duct, which passes under the albumen gland and curves again between the albumen and membrane glands. At this point a small pyriform receptaculum seminis joins the duct. The duct curves again and joins the genital aperture at the junction of the duct of the bursa copulatrix and the nidamental glands. The bursa is thin-walled and spherical. From the genital aperture, the ciliated sperm groove transports endogenous sperm to the penis, situated on the right side of the head.

The penis (Figure 10C) is similar to that of other members of the genus. The prostate is distinctly bifid in both specimens examined. Immediately anterior to the junction of the two prostatic lobes is the division into the penial

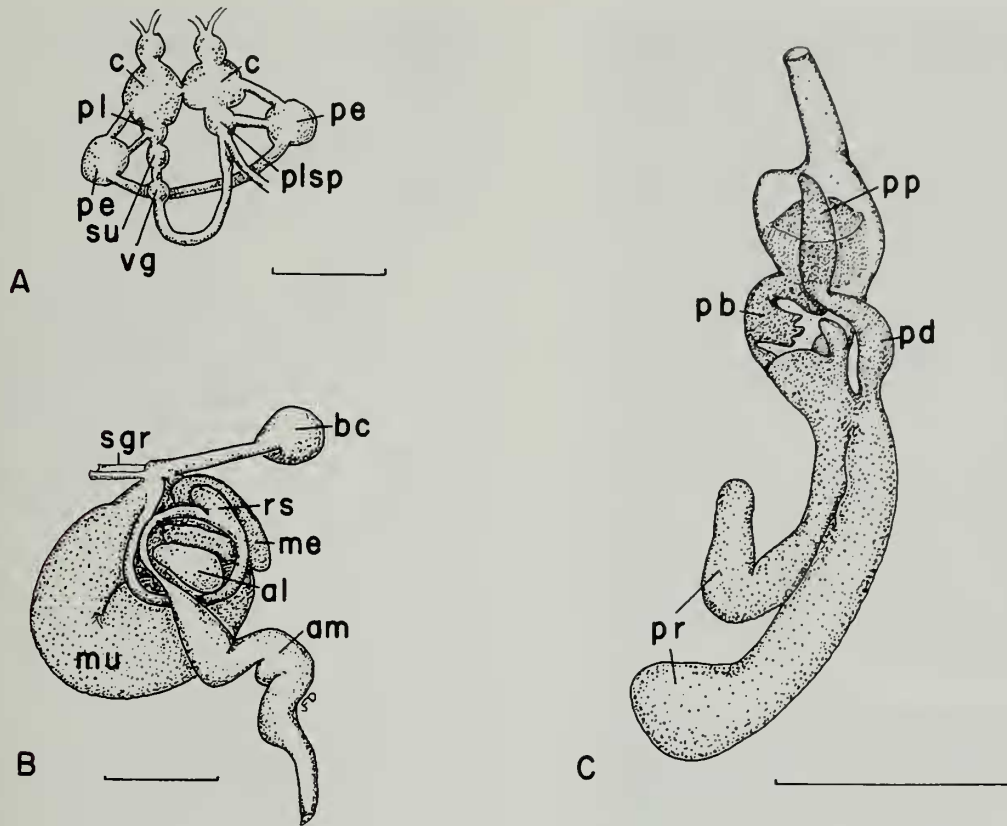


Figure 10

*Siphopteron citrinum* (Carlson & Hoff, 1974). A. Central nervous system, scale = 1.0 mm. Key: c, cerebral ganglion; pe, pedal ganglion; pl, pleural ganglion; plsp, fused pleural and suprintestinal ganglia; su, subintestinal ganglion; vg, visceral ganglion. B. Reproductive system, scale = 1.0 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. C. Penis, scale = 0.5 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla; pr, prostate.

bulb and penial duct. The penial bulb contains several muscular lobes. These lobes do not bear any rows of chitinous hooks, but do appear to have a few triangular lobes that may be enveloped by a chitinous lining. The penial duct is short and thick. At its anterior end is a short conical penial papilla that is surrounded by a cuplike layer of tissue within the penial sac. The penial papilla extends anteriorly, beyond the level of the tissue cup.

**Discussion:** The relationships of this species to *Siphopteron brunneomarginatum* and to *S. nigromarginatum* are discussed following the descriptive sections of these taxa.

*Siphopteron nigromarginatum* Gosliner, sp. nov.

(Figures 1C, 12, 13)

**Distribution:** This species is known only from the region surrounding Madang, Papua New Guinea.

**Type material:** Holotype, CASIZ 066562, SE side of Pig Island, Madang, Papua New Guinea, 10 m depth, 23 January 1988, T. M. Gosliner. One paratype, CASIZ 066565, dissected, Anemone Reef, Madang, Papua New Guinea, 3 m depth, 17 January 1988, T. M. Gosliner. One paratype, CASIZ 066563, SE side of Pig Island, Madang, Papua New Guinea, 10–12 m depth, 23 January 1988, T. M. Gosliner. One paratype, CASIZ 066564, dissected, SE side of Pig Island, Madang, Papua New Guinea, 23 January 1988, R. C. Willan. One paratype, CASIZ 066566, Planet Rock, 10 km S of Madang, Papua New Guinea, 10 m depth, 28 January 1988, T. M. Gosliner. One paratype, CASIZ 066567, dissected, Barracuda Point, Madang, Papua New Guinea, 9 m depth, 30 January 1988, T. M. Gosliner. Two paratypes, CASIZ 066568, Barracuda Point, 10–11 m depth, 7 and 8 February 1988, John Mizeu, T. M. Gosliner. One paratype, CASIZ 066569, The Quarry, 30 km N of Madang, Papua



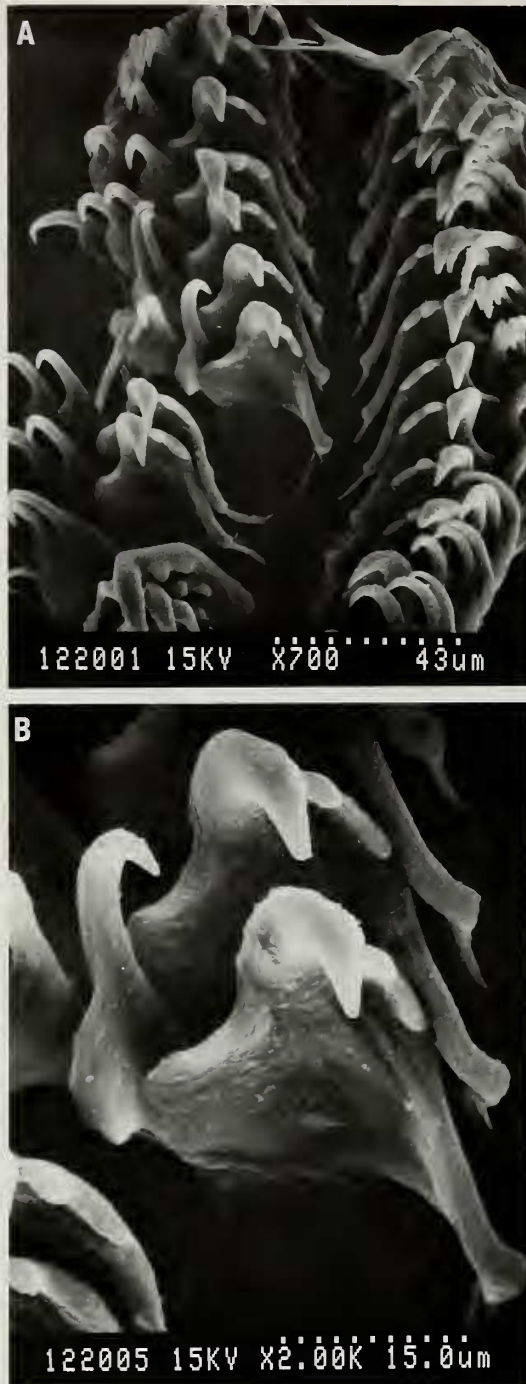


Figure 11

*Siphopteron citrinum* (Carlson & Hoff, 1974). Scanning electron micrographs. A. Radular teeth. B. Inner lateral tooth.

New Guinea, 3 m depth, 12 February 1988, T. M. Gosliner. Two paratypes, CASIZ 066579, dissected, Anemone Reef and Rasch Pass, Madang, Papua New Guinea, 4–12 m depth, 14 and 15 February 1988, T. M. Gosliner.

**Etymology:** The epithet *nigromarginatum* refers to the black pigment that ornaments the siphonal and parapodial margins of this species.

**Natural history:** Specimens of *Siphopteron nigromarginatum* have been found under stones and crawling about in the open on shallow-water reef flats and slopes. A single specimen of this species was observed swimming in the laboratory.

**External morphology:** The living animals (Figures 1C, 12A) were 3–4 mm in length. The general body color is pale yellowish white to lemon yellow. Scattered orange mottlings may be present on the head shield and visceral hump. An area of opaque white is generally present at the base of the head shield, just anterior to the beginning of the visceral hump. Black pigment adorns the apex of the siphon, the tip of the siphonal crest, the parapodial margin, and the flagellum and its base. In one specimen, black pigment was absent from the flagellum.

The head shield is roughly triangular, broadest anteriorly. Posteriorly, it attenuates to an involuted siphon, which bears a prominent medial crest with an apical papilla elevated above the remainder of the siphon. The parapodia are elongate and widest near their anterior end, never overlapping, leaving most of the visceral hump exposed. Posteriorly, the parapodia extend as low ridges almost to the posterior end of the foot. The visceral hump is ovoid, broadest posteriorly. Anterodorsal of the posterior end of the visceral hump and to the right of the midline is an elongate, conical flagellum. In the holotype, the flagellum is bifurcate, whereas in the remainder of specimens it is uniramous. The gill is situated at the base of the ridge that terminates as the flagellum. It consists of 3 or 4 simply plicate lamellae. A distinct ridge extends from the anterodorsal surface of the ctenidium to the base of the flagellum. The foot is elongate, narrowest posteriorly. A large pedal gland is present in its posterior portion.

**Digestive system:** The buccal mass is elongate and weakly muscular. At the anteroventral end of the buccal mass is a large ventral oral gland. The esophagus is narrow and expands into a thin, saccate crop. At the junction of the esophagus with the posterior end of the buccal mass is a pair of thin, cylindrical salivary glands. Within the buccal mass there are no distinctly thickened jaws. The radular formula is  $17-18 \times 3 \cdot 1 \cdot 0 \cdot 1 \cdot 3$  (Figure 13A) in three specimens examined. The inner lateral teeth (Figure 13C, D) are broad with a strong inner limb and an expanded outer lobe. Each inner lateral has a simply hooked cusp; a masticatory margin may bear a single triangular denticle on the outer end, adjacent to the central cusp (Figure 13D), and a series of 5–18 small, irregular denticles on its inner side. The large triangular denticle appears to be a result of the fusion of several smaller denticles (Figure 13C). The outer laterals (Figure 13B) are simply hook-shaped without any denticles. They possess a broad base and decrease in size towards the outer edges of the radula.

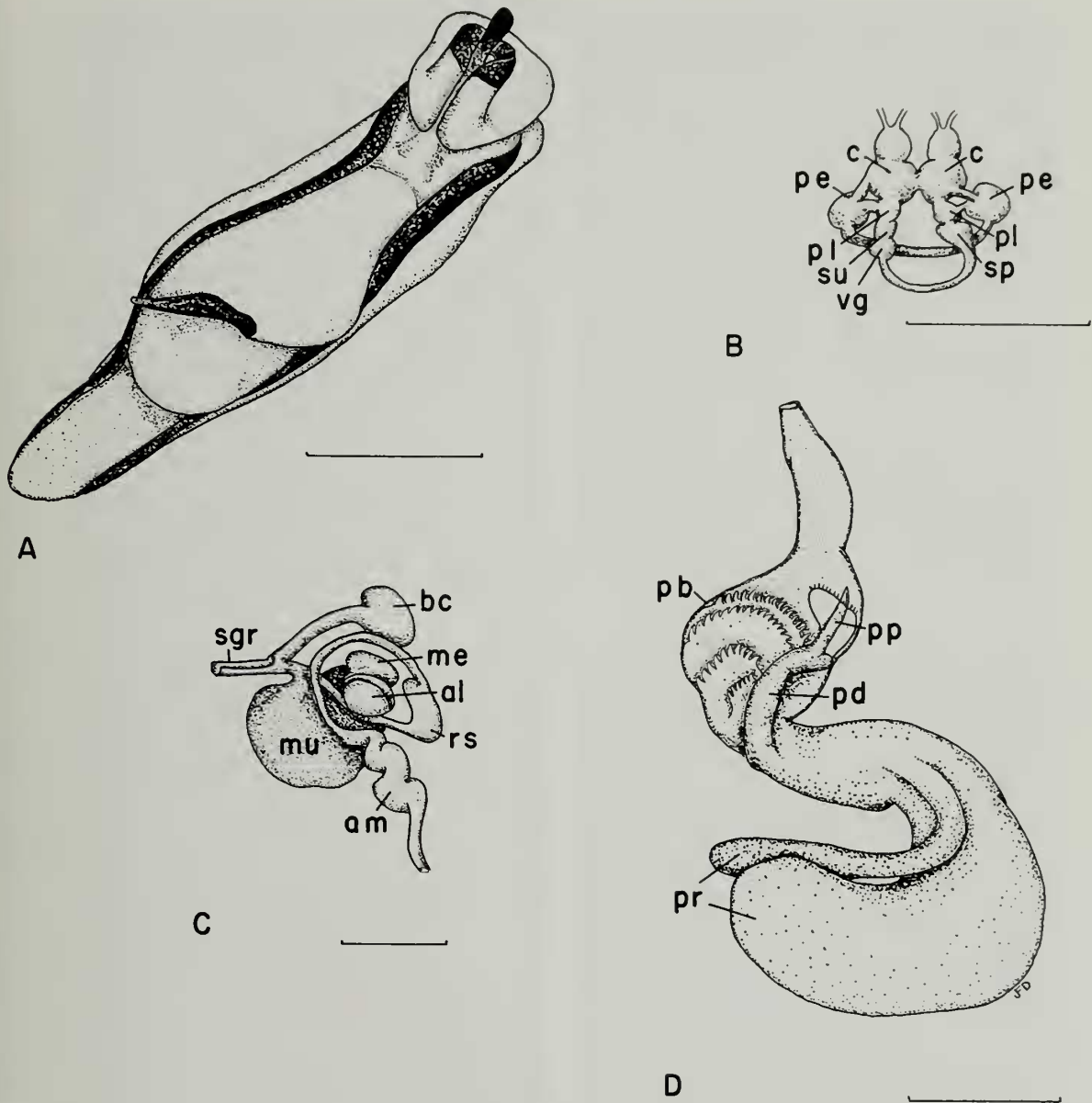


Figure 12

*Siphopteron nigromarginatum* Gosliner, sp. nov. A. Living animal, scale = 1.0 mm. B. Central nervous system, scale = 1.0 mm. Key: c, cerebral ganglion; pe, pedal ganglia; pl, pleural ganglia; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Reproductive system, scale = 0.5 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. D. Penis, scale = 0.25 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla; pr, prostate.

**Central nervous system (Figure 12B):** As in other members of the family, the arrangement of ganglia is euthyneurous with a short visceral loop. The cerebral ganglia are large, without a distinct commissure separating them. Each ganglion possesses a large anterodorsal ganglionic mass that is only slightly smaller than the ganglion proper.

Lateral and ventral to the cerebral ganglia are the large pedal ganglia. The pedal ganglia also connect with the small pleural ganglia, and are joined to each other by an elongate commissure. Posterior to the left pleural ganglion are the subintestinal and visceral ganglia. The visceral loop extends posteriorly from the visceral ganglion, curves

around the buccal mass, and joins the posterior portion of the suprainestinal ganglion.

**Reproductive system (Figure 12C):** The ampulla is narrow and convoluted. Distally from the ovotestis, it narrows into the hermaphroditic duct and curves around the large lobate mucous gland. The duct passes between the smaller albumen and membrane glands and joins the saccate receptaculum seminis. From there it continues to the hermaphroditic gonopore, where it joins the nidamental glands and the bursa copulatrix. The bursa is spherical and situated at the end of an elongate, narrow duct. From the gonopore, a ciliated sperm groove conducts spermatozoa to the cephalic penis.

The penis (Figure 12D) is elongate with a single or bilobed prostate. In three specimens the prostate was bilobed, whereas in two others it was undivided. The inner prostatic lobe, when present, is one-quarter to one-half as thick as the outer one. They may be joined for their anterior third or may be separate for almost their entire length. At the anterior end of the prostate is the bifurcation into the muscular bulb and the penial duct. The muscular bulb contains four distinct rows of chitinous spines. From posterior to anterior, there are 6, 10, 15, and 15 spines per row, respectively, in one specimen examined. The anterior end of the penial duct narrows into an elongate pointed apex that appears to be a chitinous stylet, which enters a flat papilla.

**Discussion:** The morphology of this species exhibits considerable variation. The coloration varies particularly in the amount of yellow and orange pigment present. Black pigment is present on the siphon, siphonal crest, and parapodial margins in all material examined, but was absent from the flagellum in one specimen. The flagellum is bifurcate in the holotype, but undivided in the remaining specimens. The elaboration of denticles on the inner lateral tooth exhibits various degrees of fusion in different specimens. The prostate may be single or bilobed.

*Siphopteron nigromarginatum* is similar in appearance to several other members of the genus with yellow or orange ground color ornamented with brown, black, or maroon pigment. CARLSON & HOFF (1974) compared *Siphopteron citrinum*, *S. flavum*, and *S. brunneomarginatum*. They noted that *S. citrinum* is unique in having a single triangular denticle at the inner base of the central cusp of the inner lateral teeth and that it lacked any elongate denticles.

Subsequently, GOSLINER (1984) described *Siphopteron flavobrunneum* and GOSLINER & WILLIAMS (1988) described *S. michaeli*, which have similar coloration.

Despite the external similarity of these five taxa to each other and to *Siphopteron nigromarginatum*, several consistent external and internal differences clearly separate these species. *Siphopteron michaeli* and *S. flavobrunneum* both entirely lack a flagellum. In *S. flavum* the flagellum is a medial bulb at the posterior end of the visceral hump. In *S. nigromarginatum*, *S. brunneomarginatum*, and *S.*

*citrinum*, the flagellum is elongate and situated well to the right of the medial line of the body. In *S. brunneomarginatum* the parapodia touch or overlap each other whereas in *S. citrinum* and *S. nigromarginatum* they are well separated. Swimming has been observed in *S. citrinum* and *S. nigromarginatum*, but not in *S. brunneomarginatum*. Most importantly, the penis of *S. nigromarginatum* bears several rows of chitinous spines, whereas *S. brunneomarginatum* and *S. citrinum* entirely lack penial spines.

In its external appearance, *Siphopteron nigromarginatum* is most similar to *S. citrinum*. In fact, specimens from Papua New Guinea were originally thought to be conspecific with *S. citrinum*. However, several consistent external and internal differences clearly distinguish the two species. Specimens of *S. nigromarginatum* always have black pigment on the margins of the parapodia and along the apical margin of the siphon. *Siphopteron citrinum* lacks black parapodial margins and black pigment is restricted to the apex of the siphonal crest, but is absent from the apical margins of the siphon. In both *S. nigromarginatum* and *S. citrinum* there is a distinct ridge from the dorsal surface of the gill to the flagellum.

The inner lateral teeth of *Siphopteron citrinum* have only a single denticle in addition to the elongate cusp, whereas in *S. nigromarginatum* there are more denticles. However, in the latter species these may exhibit some fusion of denticles to form triangular cusps.

In the central nervous system of *Siphopteron nigromarginatum*, the left pleural, subintestinal, and visceral ganglia are all appressed to each other, whereas in *S. citrinum* there is a gap between the subintestinal and visceral ganglia. In *S. citrinum* the suprainestinal and right pleural ganglia are largely fused, but in *S. nigromarginatum* they are distinct.

The most significant differences between the two species are in their penial morphology. In *Siphopteron nigromarginatum* distinct rows of chitinous spines line the penial bulb, whereas spines are entirely absent in *S. citrinum*. The penial papilla is thin and elongate in *S. nigromarginatum* and barely protrudes into a conical fleshy area. In *S. citrinum*, the papilla is short and fleshy, but extends well beyond a cuplike structure.

Based on these consistent differences within several organ systems, *Siphopteron nigromarginatum* and *S. citrinum* are considered as distinct species.

*Siphopteron pohnpei* (Hoff & Carlson, 1983)

(Figures 1D, 14, 15)

*Gastropteron pohnpei* HOFF & CARLSON, 1983:261, figs. 1-3.

*Siphopteron pohnpei* (Hoff & Carlson, 1983) comb. nov.

**Distribution:** This species is known from Ponape and Palau (HOFF & CARLSON, 1983) and Oahu, Hawaiian Islands (present study).

**Material:** One specimen, partially dissected, California



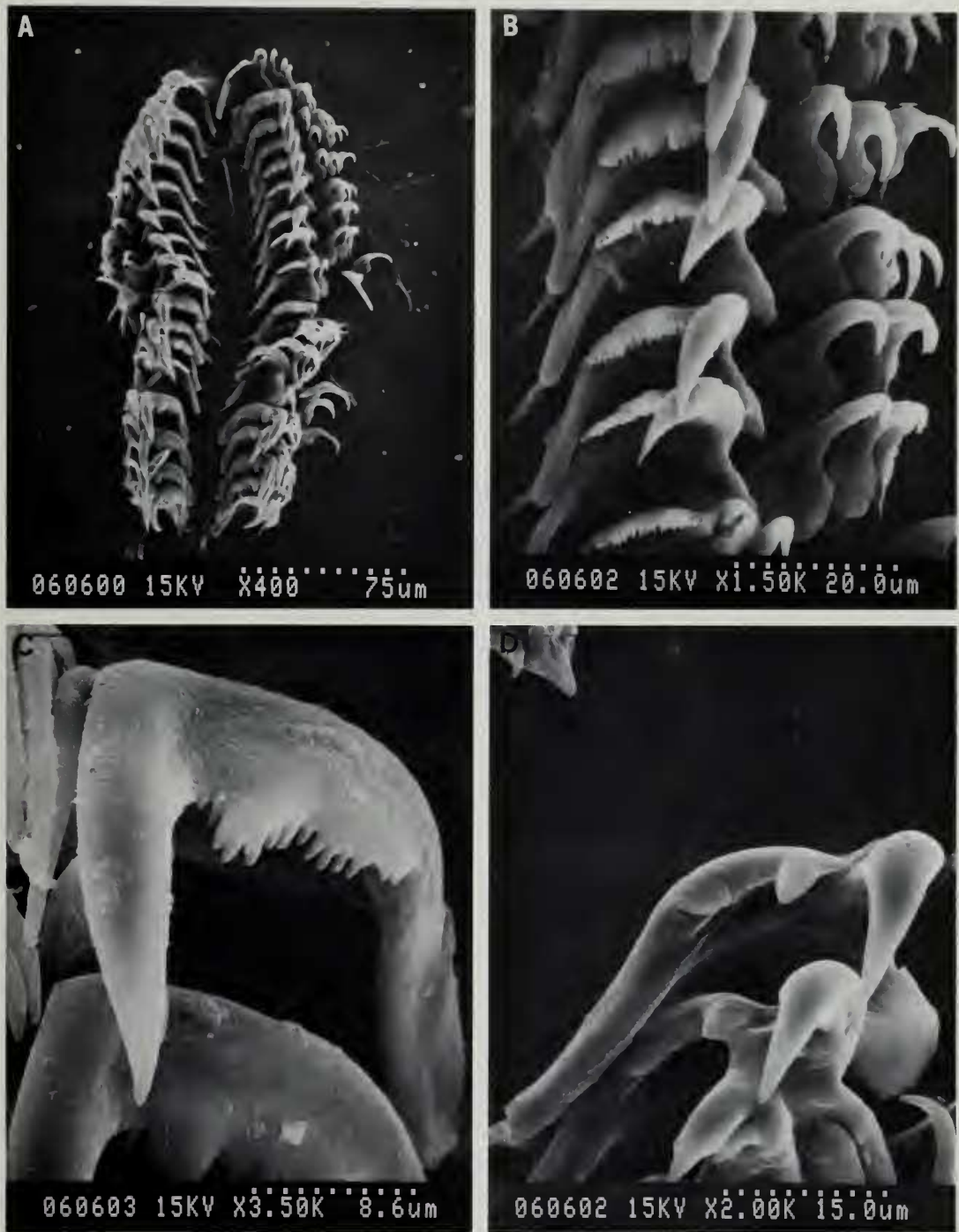


Figure 13

*Siphopteron nigromarginatum* Gosliner, sp. nov. Scanning electron micrographs. A. Entire radula. B. Half-row of radular teeth. C. Inner lateral tooth. D. Inner lateral tooth.

Academy of Sciences, San Francisco, CASIZ 066571, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 13 February 1986, 15 m depth, M. T. Ghiselin. One specimen, CASIZ 066572, dissected, Sand Island, Kaneohe Bay,

Oahu, Hawaiian Islands, 13 February 1986, 15 m depth, T. M. Gosliner. Three specimens, CASIZ 066573, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 3 m depth, 10 September 1987, T. M. Gosliner. One specimen, CA-

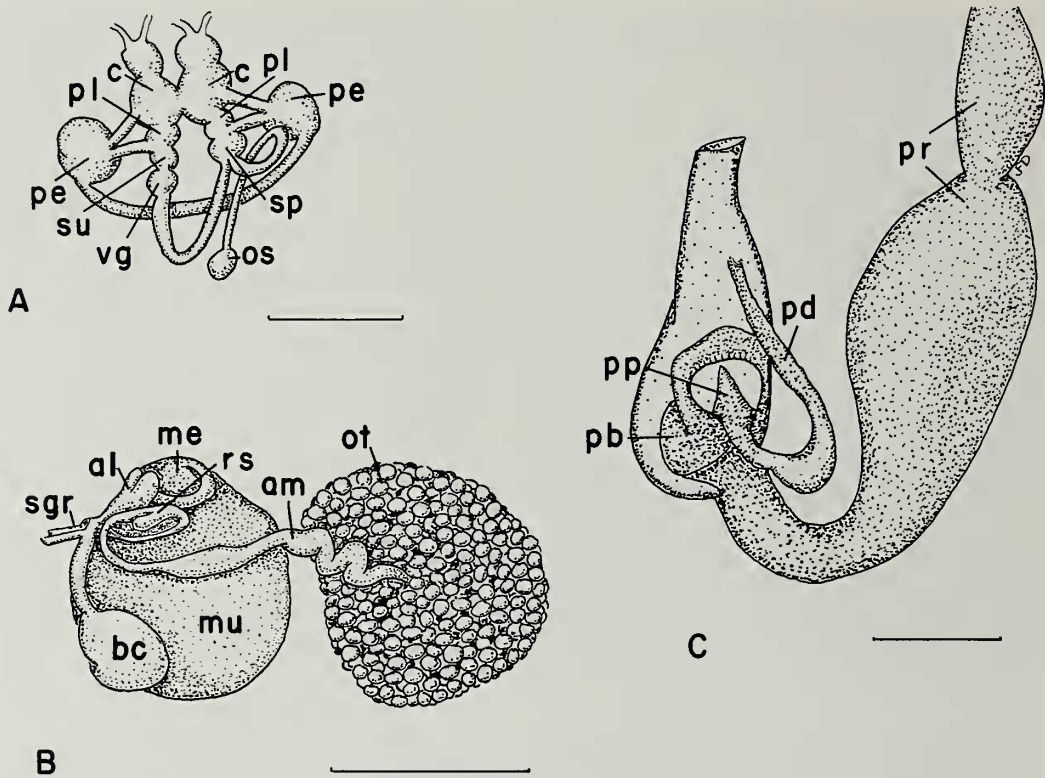


Figure 14

*Siphopteron pohnppei* (Hoff & Carlson, 1983). A. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglion; os, osphradial ganglion; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. B. Reproductive system, scale = 1.0 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; ot, ovotestis; rs, receptaculum seminis; sgr, sperm groove. C. Penis with constricted prostate, scale = 0.1 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla.

SIZ 066574, dissected, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 3 m depth, 10 September 1987, T. M. Gosliner. Two specimens, both dissected, CASIZ 066575, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 10 September 1987, 3 m depth, T. M. Gosliner.

**Natural history:** Specimens have been found commonly inhabiting shallow subtidal sand flats in Kaneohe Bay, together with *Siphopteron quadrispinosum* sp. nov. The animals are capable of swimming by flapping their large parapodia.

**External morphology:** The living animals (Figure 1D) are 3–5 mm in length. The general body color is variable and ranges from brown to red. Brownish animals were observed to copulate with red ones. Animals with brown color may also have opaque white and yellow spots. Frequently, brown pigment is absent from the posterior end of the foot, leaving a translucent area on the posterodorsal portion of the animal. The head shield is short and triangular with an involuted siphon at its posterodorsal limit. The siphon contains a medial crest that terminates in an

elongate, cylindrical extension. The visceral hump is elongate, ovoid with no flagellum or other elaboration in any of the observed specimens. The parapodia are well developed. The gill is situated on the right side of the body, ventral to a prominent crescentic ridge. It is minutely bipinnate, consisting of six primary leaflets.

**Digestive system:** The buccal mass is well developed and muscular. Anteroventral to the buccal mass is a prominent oral gland. At the junction of the esophagus with the posterior end of the buccal mass is a pair of large, ventrally reflexed salivary glands. No chitinous rodlets were observed on the jaws of the lining of the buccal mass. The radular formula was  $17-19 \times 4 \cdot 1 \cdot 0 \cdot 1 \cdot 4$  in the two specimens observed. The inner lateral teeth (Figure 15C, D) are broad with an elongate central cusp. On the inner side of the cusp is a thick ridge bearing 8–10 elongate denticles. The outer laterals (Figure 15A, B) are also broad with a wing on their inner surface.

**Central nervous system:** The arrangement of ganglia (Figure 14A) is essentially identical to that described for



Figure 15

*Siphopteron pohnpei* (Hoff & Carlson, 1983). Scanning electron micrographs. A. Half-row of radular teeth of brown specimen. B. Half-row of radular teeth from red specimen. C. Inner lateral teeth of brown specimen. D. Inner lateral teeth of red specimen.



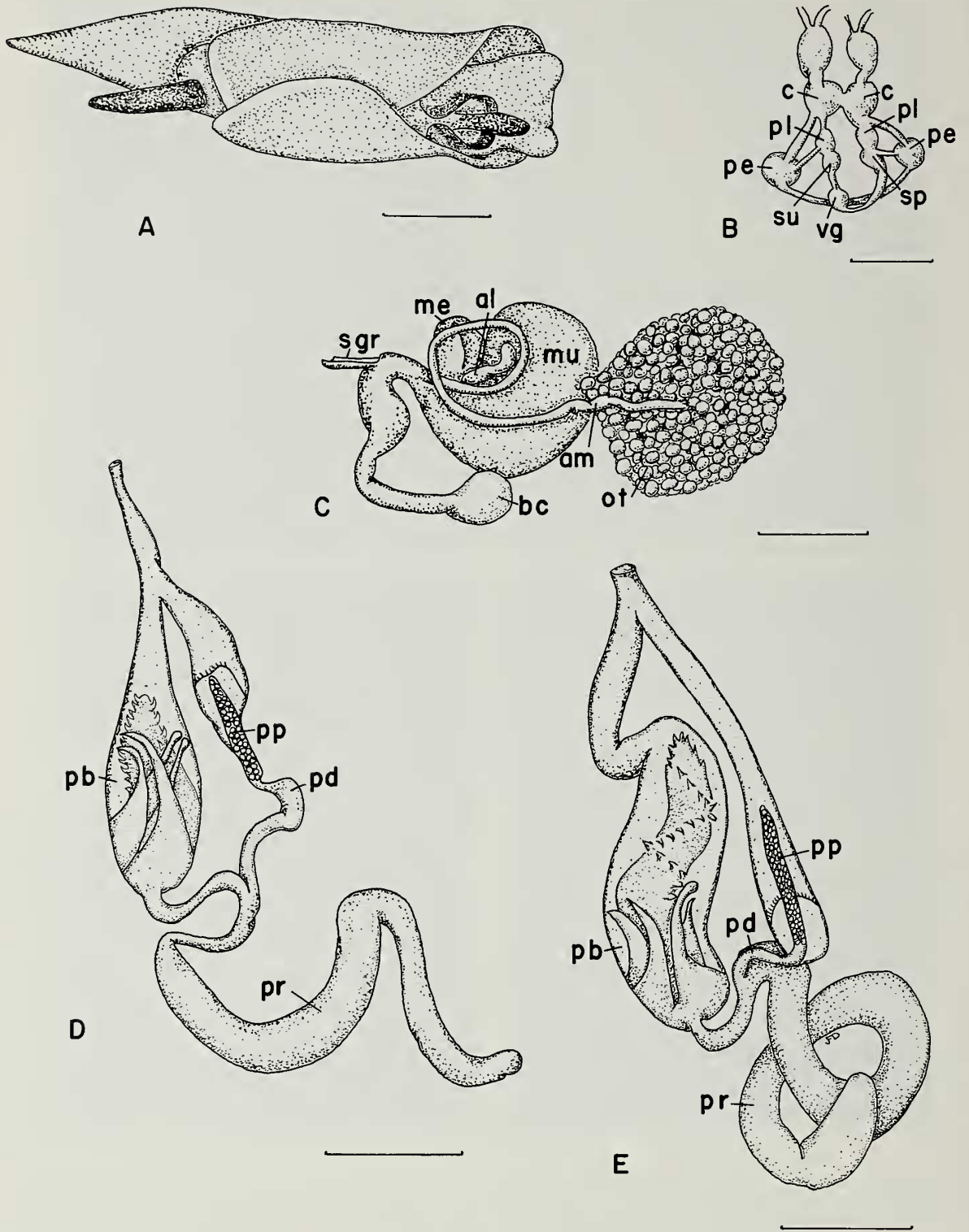


Figure 16

*Siphopteron quadrispinosum* Gosliner, sp. nov. A. Dorsal view of living animal, scale = 1.0 mm. B. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglion; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Reproductive system, scale = 0.5 mm. Key: al, albumen

*Siphopteron brunneomarginatum* above. The only exception is that a distinct osphradial ganglion was observed in *S. pohnpei*, and that its pedal ganglia appear larger than the cerebral ganglia.

**Reproductive system:** The organs are arranged in a monaulic fashion (Figure 14B). The ovotestis consists of numerous acini, arranged in a discoidal fashion. From the ovotestis a narrow preampullary duct expands into a highly convoluted ampulla. Distally, the ampulla narrows into the hermaphroditic duct. The hermaphroditic duct recedes near the basal portion of the albumen gland and expands and contracts again immediately proximal to the short, bulbous receptaculum seminis. More distally, the hermaphroditic duct again curves and joins the genital aperture together with the albumen, membrane, and mucous glands and the duct of the spherical bursa copulatrix. There is no separate duct from the hermaphroditic duct to the female glands, other than at the genital atrium. From the atrium, the ciliated sperm groove conducts endogenous sperm to the penis situated in the head.

The penis (Figure 14C) is complex in structure. In two specimens (one brown and one red) the proximal portion of the prostate was distinctly constricted, whereas in another two it was not. The prostate narrows distally and joins the unarmed, muscular penial bulb. Distal to the penial bulb is the penial papilla. From its proximal end a narrow duct curves distally to the distal portion of the penial sac.

**Egg mass:** The egg mass of *Siphopteron pohnpei* is a small spherical structure containing approximately 100 small white eggs. There is a single egg per capsule.

**Discussion:** *Siphopteron pohnpei* is known only from its original description (HOFF & CARLSON, 1983). The brown specimens from the present material closely resemble the original description. Initially, the brown and red specimens appeared to represent two distinct species. However, all aspects of the external and internal morphology are identical in both color phases. This, combined with the fact that both color forms copulate readily with each other, suggests that they are all members of a single, variable species.

The radular morphology is identical in the specimens from Ponape and Hawaii.

The morphology of the penis, as noted above, is similar to that of *Siphopteron brunneomarginatum* and *S. citrinum*.

The eggs, unlike those of other known members of the genus, are white rather than yellow.

*Siphopteron quadrispinosum* Gosliner, sp. nov.

(Figures 1E, 16, 17)

**Distribution:** This species has been found only in the Hawaiian Islands (from Hookena, Kona coast of Hawaii, Jeff Hamann, pers. comm.; from Molikini Crater off Lanai, Mike Severns and Pauline Fiene, pers. comm.; and from Kaneohe Bay on Oahu) and from Madang, Papua New Guinea.

**Type material:** Holotype, California Academy of Sciences, San Francisco, CASIZ 066576, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 3 m depth, 10 September 1987, T. M. Gosliner. Forty paratypes, CASIZ 066577, same locality and date as holotype, T. M. Gosliner and M. T. Ghiselin. One paratype, CASIZ 066578, dissected, same date and locality as holotype. One paratype, CASIZ 066579, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 2 m depth, 25 October 1986, T. M. Gosliner. One paratype, CASIZ 066580, Cement Mixer Reef, Madang, Papua New Guinea, 19 October 1986, 3 m depth, T. M. Gosliner. One paratype, CASIZ 066581, The Quarry, N of Madang, Papua New Guinea, 10 m depth, 11 February 1988, T. M. Gosliner.

**Etymology:** The epithet *quadrispinosum* refers to the four prominent chitinous spines in the penial bulb, which characterize this species.

**Natural history:** The living animals are found most commonly on sand flats from shallow water (2–3 m depth) to depths of 30 m. In Papua New Guinea, two specimens were collected on the undersides of dead coral heads. The animals are capable of swimming for prolonged periods of time (up to 5 minutes) by flapping their parapodia.

**External morphology:** The living animals (Figures 1E, 16A) are 3–5 mm in length. The general body color is bright yellow. The siphon and flagellum are red-orange. In the specimens from Papua New Guinea, the red-orange pigment continues from the siphon along the posterior margin of the head shield and from the flagellum as a transverse line on the dorsal surface of the visceral hump. Also, in the New Guinea specimens, much of the visceral hump is milky white, rather than being uniformly yellow. In the Hawaiian specimens, the parapodial margin is opaque white, whereas it is uniformly yellow in the New Guinea specimens.

The head shield (Figure 16A) is triangular, rounded anteriorly, and terminating posteriorly as an involuted

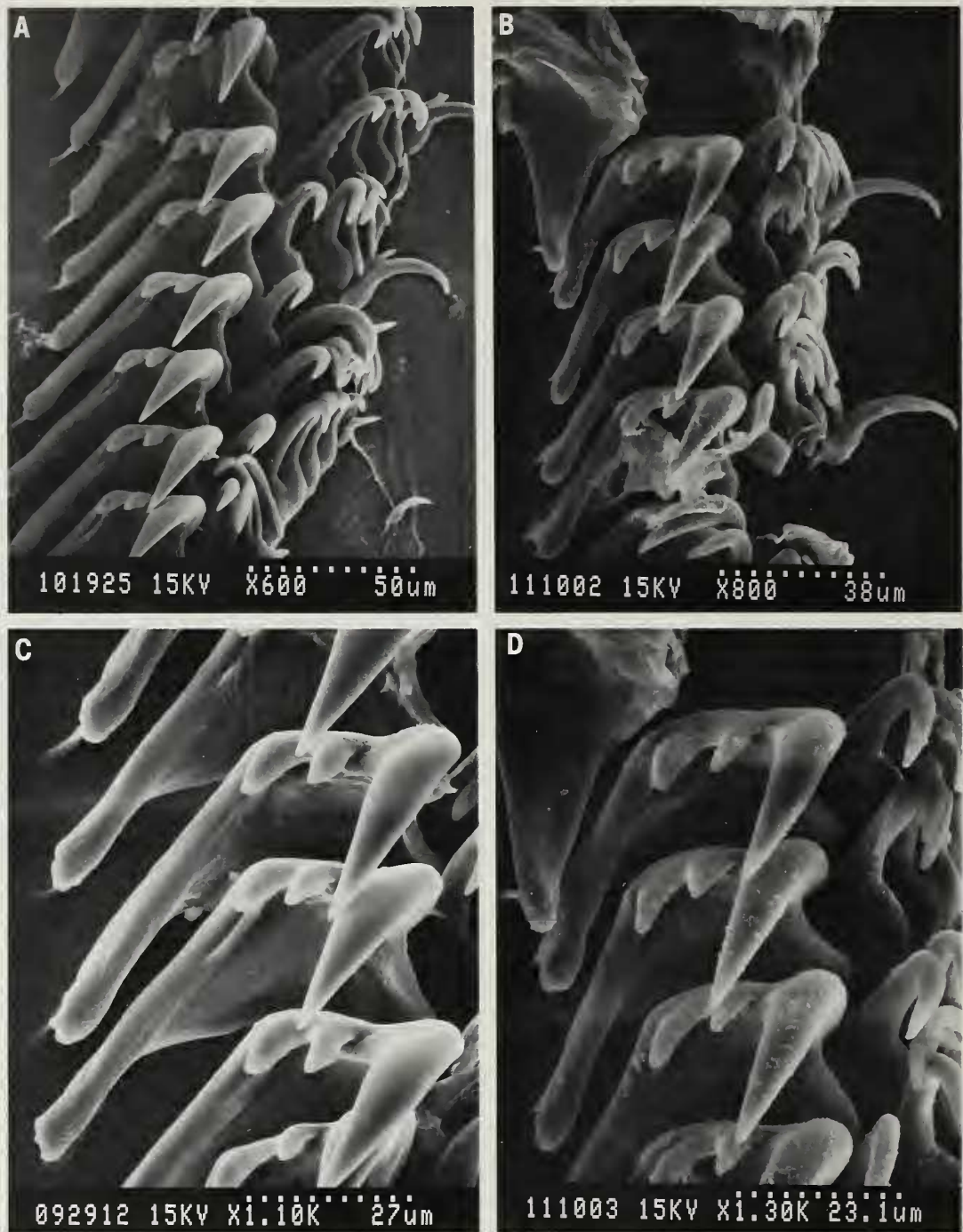


Figure 17

*Siphopteron quadrispinosum* Gosliner, sp. nov. Scanning electron micrographs. A. Half-row of radular teeth of Hawaiian specimen. B. Half-row of radular teeth of Papua New Guinea specimen. C. Inner lateral teeth of Hawaiian specimen. D. Inner lateral teeth of Papua New Guinea specimen.



siphon. The siphon has a prominent medial crest terminating in a papilla that extends above the level of the rest of the siphon. The visceral hump is elongate and ovoid with an elongate, acutely pointed posterior flagellum, situated just to the right of the midline. The parapodia are elongate and are sufficiently high that in resting animals the margins of the parapodia overlap. In preserved specimens it is possible to see numerous small glands along the outer third of the parapodia. The foot is elongate and acutely pointed posteriorly. A large ovoid pedal gland is present on the ventral surface of the foot. The gill, situated on the right side of the body, consists of 4–6 simple plicae.

**Digestive system:** The buccal mass is large and muscular. A small ventral oral gland is present at the anteroventral margin of the buccal mass. Paired, convoluted salivary glands are present at the junction of the esophagus with the posterior end of the buccal mass. Jaws bearing five or six rows of chitinous rodlets are contained within the anterior portion of the buccal mass. The radular formula in two specimens was  $18-20 \times 4-6 \cdot 1 \cdot 0 \cdot 1 \cdot 4-6$ . The inner lateral teeth (Figure 17C, D) are broad with an elongate cusp. A pair of triangular cusps is present on the inner masticatory margin. The outer lateral teeth (Figure 17A, B) are simple, hook-shaped, and without denticles. They decrease in size towards the outer margin.

**Central nervous system:** The arrangement of ganglia (Figure 16B) is virtually identical to that described for *Siphopteron brunneomarginatum*.

**Reproductive system:** The arrangement of organs (Figure 16C) is monaulic. The large, discoidal ovotestis consist of numerous acini. The preampullary duct is narrow and does not expand dramatically as it becomes the slightly convoluted ampulla. The ampulla narrows as it becomes the hermaphroditic duct and wraps around the albumen and membrane glands. A distinct receptaculum appears to be absent. The hermaphroditic duct curves distally between the membrane, albumen, and mucous glands and joins the widened genital atrium. The spherical bursa copulatrix has a narrow duct, which triples its width in the ectal third of its length.

The structure of the complex penis (Figure 16D, E) was examined in three specimens. The prostate is elongate with two or three major convolutions. Distally, it narrows for a variable portion of its length. Prior to its junction with the penial bulb, a narrow duct emerges and runs to the penial papilla. There is an elongate and reticulate spine in the penial papilla. The apex of the fleshy portion is rounded and ciliated. Within the penial bulb are four large, gold chitinous spines. The apices of two of these are capitate and the other two are acutely curved. More distally, there is a fleshy papilla, which is ornamented with a row of spines on either margin. There are 11 or 12 spines on the inner side and 3 or 4 spines on the outer side in the two Hawaiian animals examined. In the specimen from

Papua New Guinea, there are two rows of spirally arranged spines with 12 spines on the inner side and 19 on the outer one. The spiral arrangement is likely due to partial contraction of the papilla. The penial bulb and penial papilla join near the distal end of the penial aperture.

**Egg mass:** The egg mass is spherical with numerous yellow, individually encapsulated eggs.

**Discussion:** The external and internal morphology of the animals from the Hawaiian Islands is remarkably consistent in the greater than fifty specimens observed. The specimens from Papua New Guinea differ from the Hawaiian animals in several small aspects of their color and in the arrangement of penial spines. The fact that they are similar in radular morphology and in the remainder of the detailed structure of the penis suggests that they are indeed conspecific. Examination of more material from the western Pacific is required to ensure that this is a single widespread species rather than a species pair.

The radular morphology, with a pair of triangular denticles on the inner surface of the inner lateral tooth, is similar to that found in *Sagaminopteron* Tokioka & Baba, 1964 (TOKIOKA & BABA, 1964; CARLSON & HOFF, 1973, 1974; present study). However, species of *Sagaminopteron* can be distinguished from members of *Siphopteron* by the presence of a large bipinnate or tripinnate ctenidium, broader, more numerous outer lateral teeth, and simple penis. The fact that *Siphopteron quadrispinosum* has a separate duct leading to a distinct penial papilla confirms that it is more closely allied to other Indo-Pacific species of *Siphopteron* than to *Sagaminopteron*.

*Siphopteron quadrispinosum* can be distinguished from all other Gastropteridae by its yellow body color with red-orange siphon and flagellum. It is the only species of *Siphopteron* known to possess consistently a pair of triangular denticles on the inner margin of the inner lateral tooth. Some specimens of *S. nigromarginatum* appear to have two triangular denticles, but the scanning electron microscope reveals that these are fusions of small denticles. Its penial morphology, with three different sets of cuticular spines, is unique among known members of the Gastropteridae.

*Siphopteron tigrinum* Gosliner, sp. nov.

(Figures 1F, 18–20)

**Distribution:** This species is known from Palau (Clay Carlson and Patty Jo Hoff, pers. comm.), Queensland, Australia (Richard Willan, pers. comm.), Tulear, Madagascar (present study), and Papua New Guinea (present study).

**Type material:** Holotype, California Academy of Sciences, San Francisco, CASIZ 064343, Cement Mixer Reef, Madang, Papua New Guinea, 2 m depth, 20 October

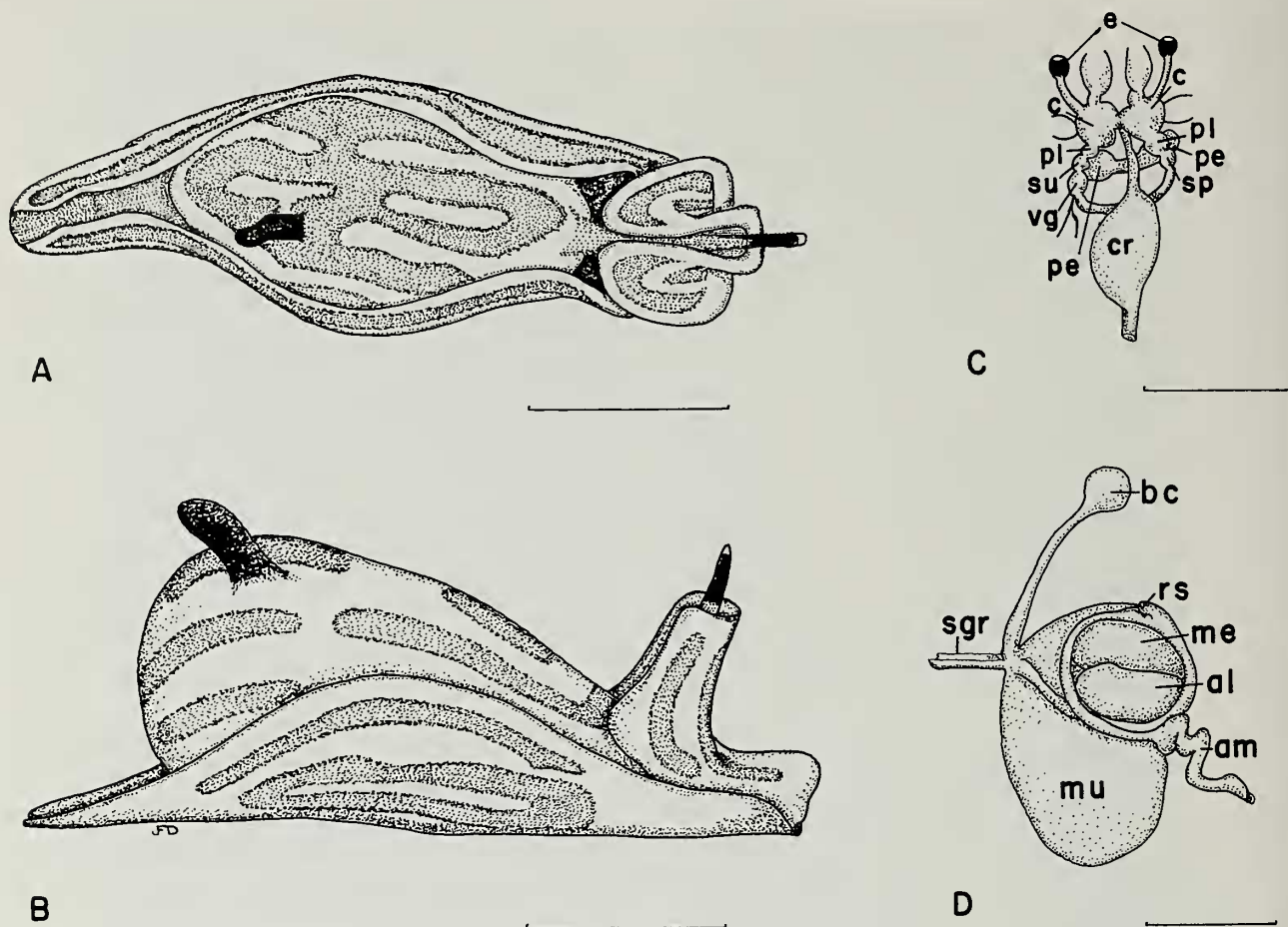


Figure 18

*Siphopteron tigrinum* Gosliner sp. nov. A. Dorsal view of predominately blue living animal, scale = 1.0 mm. B. Lateral view of predominantly orange living animal, scale = 1.0 mm. C. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglion; cr, crop; e, eye; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. D. Reproductive system, scale = 0.5 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove.

1986, T. M. Gosliner. Two paratypes, CASIZ 064344, Cement Mixer Reef, Madang, Papua New Guinea, 2 m depth, 20 October 1986, T. M. Gosliner. One paratype, CASIZ 066582, dissected, Cement Mixer Reef, Madang, Papua New Guinea, 2 m depth, 20 October 1986, T. M. Gosliner. One paratype, CASIZ 066345, dissected, Cement Mixer Reef, Madang, Papua New Guinea, 3 m depth, 22 October 1986, T. M. Gosliner. Paratype, one specimen, Sek Passage, Madang, Papua New Guinea, 27 October 1986, Michael T. Ghiselin. Two paratypes, CASIZ 066583, Barracuda Point, Madang, Papua New Guinea, 10 m depth, 8 February 1988, J. Mizeu. Four paratypes, CASIZ 066584, SE side of Pig Island, Madang, Papua New Guinea, 10 m depth, 23 and 24 January 1988, T. M. Gosliner. One paratype, CASIZ 066585, Rempi La-

goon, N of Madang, Papua New Guinea, 6 m depth, 3 February 1988, T. M. Gosliner. Two paratypes, CASIZ 066586, The Pinnacle, Madang, Papua New Guinea, 10 m depth, 25 January 1988, T. M. Gosliner. One paratype, CASIZ 066587, The Chimney, Madang, Papua New Guinea, 17 m depth, 30 January 1988, G. Williamson. One paratype, CASIZ 066588, N side Kranket Island, Madang, Papua New Guinea, 10 m depth, 24 January 1988, T. M. Gosliner. One paratype, CASIZ 066589, S side of Rasch Passage, Madang, Papua New Guinea, 8 m depth, 14 February 1988, R. C. Willian. Two paratypes, CASIZ 066590, Sek Passage, Madang, Papua New Guinea, 11 m depth, 21 February 1988, T. M. Gosliner. One paratype, CASIZ 066591, Madang Light, Madang, Papua New Guinea, 12 m depth, 1 February 1988, T.

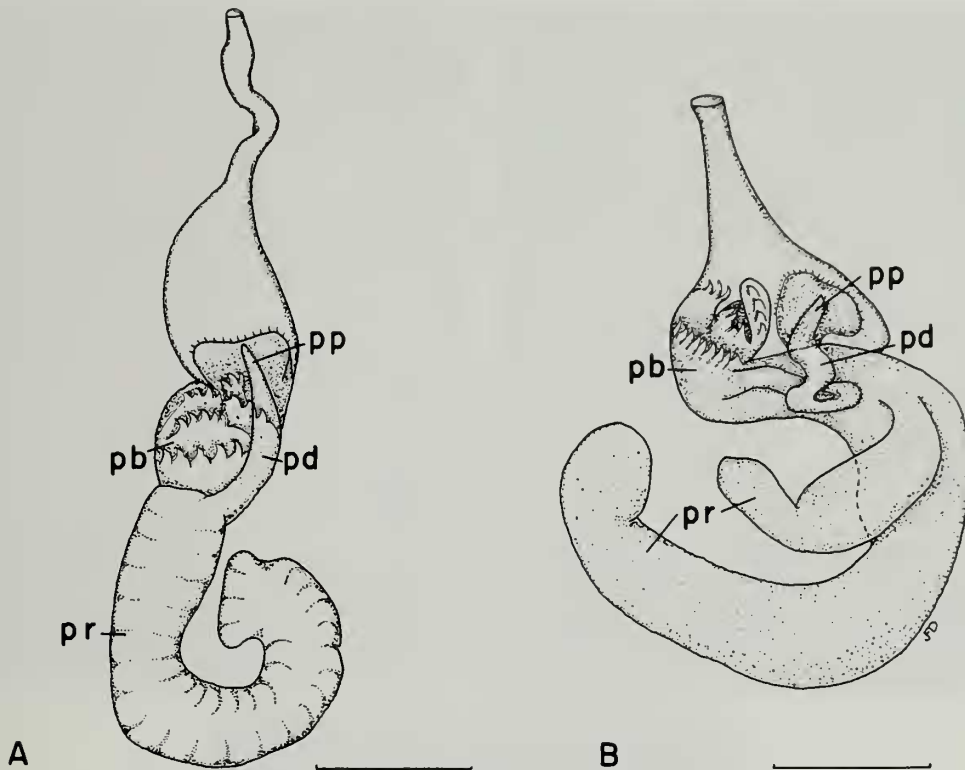


Figure 19

*Siphopteron tigrinum* Gosliner, sp. nov. A. Penis with undivided prostate, scale = 0.2 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla; pr, prostate. B. Penis with bilobed prostate, scale = 0.2 mm. Key: Lettering as in A.

M. Gosliner. One paratype, CASIZ 066592, Sek Passage, Madang, Papua New Guinea, 9 m depth, 1 February 1988, T. M. Gosliner.

**Etymology:** The epithet *tigrinum* refers to the striped pattern of coloration, resembling that of a tiger.

**Natural history:** Specimens have been found commonly on the under surface of coral rubble, on shallow reefs. It is the most abundant species of gastropterid in Madang, Papua New Guinea, where it has been found together with *Siphopteron nigromarginatum*, *Siphopteron brunneomarginatum*, *Siphopteron quadrispinosum*, and *Sagaminopteron psychedelicum*. This species has never been observed to swim.

**External morphology:** The living animals (Figures 1F, 18A, B) are 3–4 mm in length. The ground color is brilliant orange. The head shield, visceral hump, and outer surfaces of the parapodia possess narrow, elongate blue patches, surrounded by a narrow line of purplish blue. On the dorsal surface of the foot a yellowish triangular patch is present. The apex of the siphon, at the posterior end of the head shield, and the entire length of the posterior flagellum are black.

The head shield is short, roughly triangular. The posterior end of the shield is involuted, forming a distinct siphon. A prominent medial crest within the siphon terminates in an elevated papilla. The visceral hump is rounded posteriorly. Near its posterior end, on the right half of the body, is an elongate, conical flagellum. The parapodia are elongate, reaching the middle of the visceral hump in height. They are not distinctly separated from the foot. Posteriorly, the foot is elongate and triangular. The ventral surface of the foot contains an elongate pedal gland near its posterior limit. On the right side of the visceral hump is the simply plicate ctenidium, consisting of 3 or 4 leaflets.

**Digestive system:** The muscular buccal mass is short and bulbous. A large oral gland is present ventral to the buccal mass. Within the buccal mass is a thin cuticular lining, devoid of any jaw rodlets. The radular formula is  $20 \times 3 \cdot 1 \cdot 0 \cdot 1 \cdot 3$  in two specimens examined. The inner lateral teeth (Figure 20C) are broad with an elongate curved cusp. On the inner side of the tooth is a short masticatory margin, which may bear up to eight irregular denticles or may be entirely smooth. The outer lateral teeth (Figure 20A, B) have a short triangular base and an elongate curved cusp. The width of the base of the teeth decreases towards the



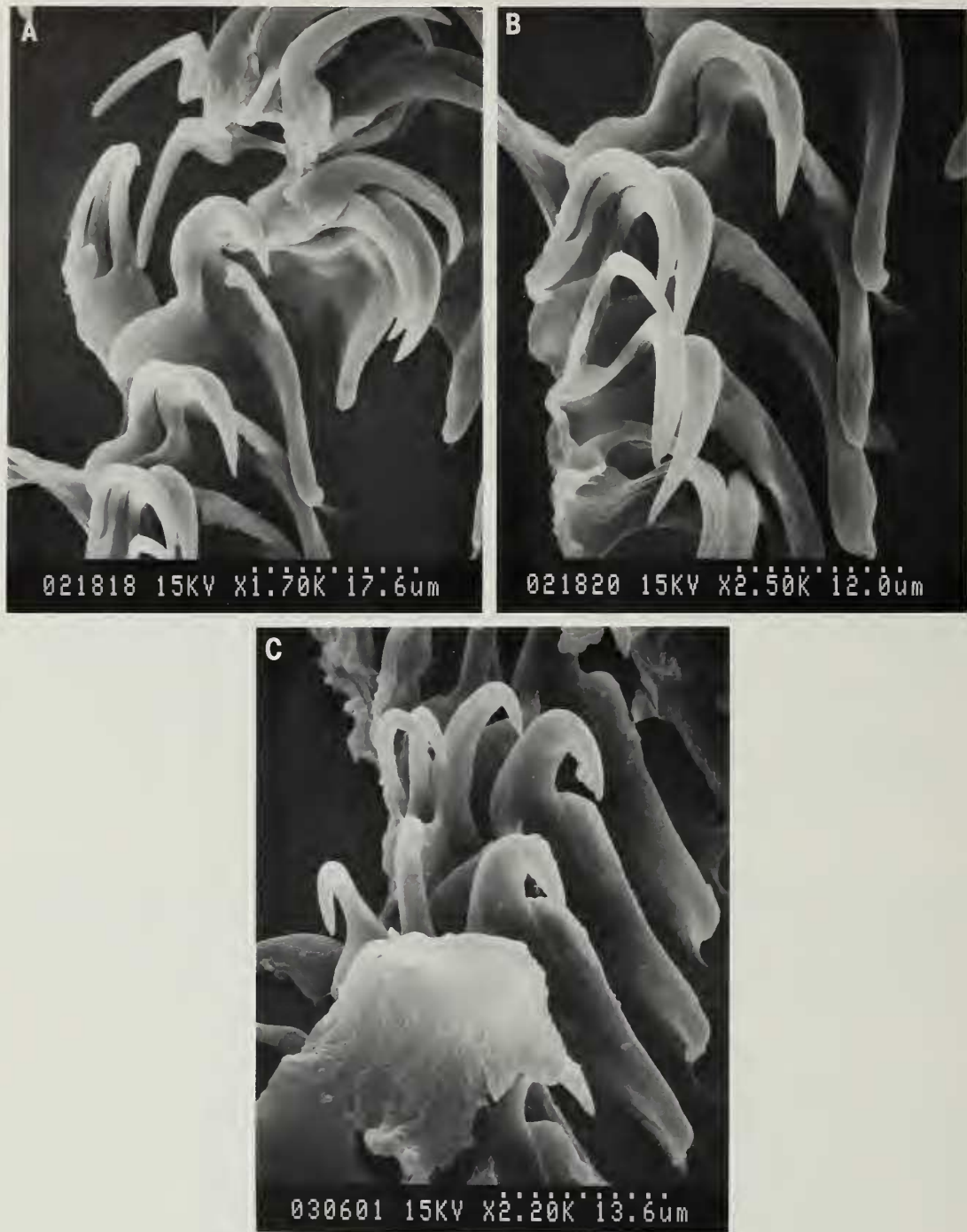


Figure 20

*Siphopteron tigrinum* Gosliner, sp. nov. Scanning electron micrographs. A. Half-row of radular teeth. B. Half-row of radular teeth. C. Inner lateral teeth.

outer margin of the radula. No denticles are on the outer laterals.

Extending from the posterior end of the buccal mass is a short narrow esophagus. At the juncture of the esophagus with the buccal mass is a pair of large salivary glands. The esophagus expands into a bulbous thin-walled crop.

**Central nervous system (Figure 18C):** All of the ganglia of the euthyneurous nervous system are situated within the circumesophageal nerve ring. The large cerebral ganglia are appressed to each other, without a distinct commissure. Extending dorsally from the cerebral ganglia are thickenings of nervous tissue, which are almost as large as the ganglia. Adjacent to these thickenings are the optic nerves, with a large eye at each apex. The pedal ganglia are slightly smaller than the cerebrals and are ventral to them. They are separated by a commissure, the length of which is approximately equal to the diameter of the pedal ganglion. Immediately posterior to the right cerebral ganglion is the right pleural ganglion. The suprainestinal ganglion is directly posterior to the right pleural. From its posterior end emerges the visceral nerve. The visceral nerve forms a short loop and, on the left side, joins the visceral ganglion adjacent to two other prominent nerves. The subintestinal ganglion is situated between the visceral and left pleural ganglia.

**Reproductive system (Figure 18D):** The arrangement of reproductive organs is monaulic. The ampulla is narrow and convoluted. It narrows further into the hermaphroditic duct, which encircles the albumen and membrane glands. A short sessile receptaculum seminis is situated near the outer edge of the female gland mass, near the middle of the hermaphroditic duct. The hermaphroditic duct terminates at the common gonopore, near the junction of the large mucous gland and the duct of the bursa copulatrix. The bursa is spherical and thin-walled. From the common genital opening, the ciliated sperm groove extends anteriorly to the penial aperture on the right side of the head.

The penis is large and is situated on the right and posterior sides of the buccal mass. In one specimen (Figure 19A) the prostate is thick and curved, consisting of a single lobe. In the second specimen (Figure 19B) there are two distinct prostatic lobes. The prostate enters a muscular vestibule that contains four areas of chitinous hooks. The posteriormost is a single straight row of 6–9 hooks, in the two specimens examined. Anteriorly there may be two or three rows of hooks which are embedded in large muscular flaps. There are 3–5 hooks on each of these flaps. In one specimen, an additional anterior row of seven hooks is present. From the juncture of the prostate and the vestibule a narrow duct runs anteriorly and enters the penial papilla in the penial sac proper. The papilla is broadest anteriorly and ciliated on its outer edge.

**Discussion:** *Siphopteron tigrinum* is immediately distinguishable from other members of the Gastropteridae by

its unique coloration. No other member of the family has orange coloration with blue, purple, and black ornamentation. It is similar to *S. citrinum* (CARLSON & HOFF, 1974), *S. nigromarginatum*, *S. fuscum* (BABA & TOKIOKA, 1965), *S. ladrones* (CARLSON & HOFF, 1974), and *S. quadrispinosum* sp. nov. in that it has an elongate flagellum on the right side of the body. A flagellum may be present or absent in *S. brunneomarginatum* (CARLSON & HOFF, 1974) (GOSLINER & WILLIAMS, 1988; present study).

The radular morphology is similar to that of *Siphopteron ladrones* (CARLSON & HOFF, 1974; GOSLINER, 1988a), *S. brunneomarginatum* (CARLSON & HOFF, 1974; present study) and *S. michaeli* (GOSLINER & WILLIAMS, 1988) in that the denticles of the inner lateral tooth, when present, are few in number and weakly developed. In both *S. tigrinum* and *S. michaeli*, denticles may be present or entirely absent from the masticatory margin of the inner lateral teeth.

The penial morphology of *Siphopteron tigrinum* is most similar to that of *S. nigromarginatum* (present study), *S. michaeli* (GOSLINER & WILLIAMS, 1988:fig. 2D), and *S. flavum* (Tokiooka & Baba, 1964) (present study). In all four of these species, a muscular vestibule is situated between the prostate and penial sac, which bears several transverse rows of recurved chitinous hooks. Also, a separate duct leads from the junction of the prostate and the vestibule leading to the penial papilla. The penial morphology of *S. tigrinum* is also similar to that of *S. michaeli*, *S. nigromarginatum*, and *S. brunneomarginatum* in that members of both species may have either an undivided or bilobed prostate in different individuals.

Despite the similarities in radular and penial morphology, *Siphopteron tigrinum* and *S. michaeli* can be readily distinguished. The two differ markedly in their coloration. In *S. tigrinum* there are bright blue and purple lines, whereas *S. michaeli* has large maroon spots. *Siphopteron michaeli* entirely lacks a flagellum. The right pleural and suprainestinal ganglia are distinct in *S. tigrinum*, whereas they are fused in *S. michaeli*.

### *Siphopteron flavum* (Tokiooka & Baba, 1964)

(Figures 21, 22)

*Gastropteron flavum* TOKIOKA & BABA, 1964:212, figs. 5–7, pl. 10, figs. 10–12; pl. 11, figs. 6–8; pl. 13, fig. 3; BABA & TOKIOKA, 1965:374, fig. 7D; CARLSON & HOFF, 1974:346, figs. 12E, 13A; BERTSCH & JOHNSON, 1981:18, 19, unnumbered figure.

*Siphopteron flavum* (Tokiooka & Baba, 1964) comb. nov.

**Distribution:** This species is known from Japan (TOKIOKA & BABA, 1964; BABA & TOKIOKA, 1965), GUAM (CARLSON & HOFF, 1974), and the Hawaiian Islands (BERTSCH & JOHNSON, 1981).

**Material:** Four specimens, dissected, California Academy of Sciences, San Francisco, CASIZ 066593, Bile Bay, Merizo, Guam, 6 m depth, 29 February and 16 April, 1976,



Figure 21

*Siphopteron flavum* (Tokioka & Baba, 1964). Scanning electron micrographs. A. Half-row of radular teeth. B. Inner lateral teeth of specimen from Guam. C. Half-row of radular teeth of specimen from Hawaii.



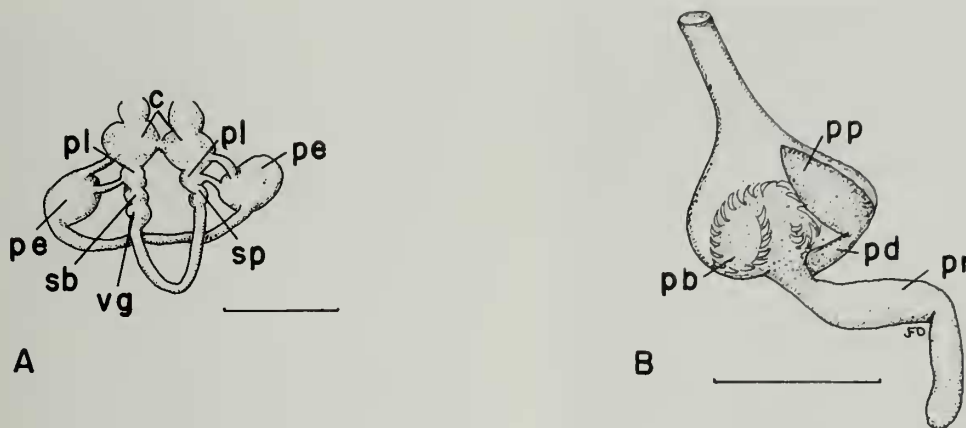


Figure 22

*Siphopteron flavum* (Tokioka & Baba, 1964). A. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglia; pe, pedal ganglion; pl, pleural ganglia; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. B. Penis, scale = 0.25 mm. Key: pb, penial bulb; pd, penial duct; pp, penial papilla; pr, prostate.

Clay Carlson and Patty Jo Hoff. One specimen, CASIZ 066594, 16 m depth, Maui, Hawaiian Islands, December 1988, Pauline Fiene.

**External morphology:** The living animals were 2–4 mm in length. Their general morphology agrees entirely with that described previously (TOKIOKA & BABA, 1964; BABA & TOKIOKA, 1965; CARLSON & HOFF, 1974).

**Digestive system:** The buccal mass is small and highly muscular. Within its anterior portion is a chitinous cuticle, devoid of distinct jaw plates. The radular formula in one 4-mm specimen was  $18 \times 3.1 \cdot 0.1 \cdot 3$ . The inner lateral teeth (Figure 21A, B) are large and broad, with a prominent, curved primary cusp. The masticatory border bears 12 or 13 irregular, triangular denticles. The outer lateral teeth (Figure 21A) are simply hook-shaped, without denticles, and decrease in size towards the outer margins of the radula.

**Central nervous system:** The arrangement of ganglia (Figure 22A) is virtually identical to other members of *Siphopteron* described here. The large cerebral ganglia are appressed to each other without a distinct commissure. They give rise to anterodorsal ganglionic thickenings. The large pedal ganglia are joined to the cerebral and pleural ganglia by short, paired commissures, and to each other by an elongate connective. Posterior to the left pleural ganglion are the subintestinal and visceral ganglia. A short visceral loop joins the visceral ganglion to the supraintestinal ganglion, which is appressed to the right pleural ganglion.

**Reproductive system:** Details of posterior reproductive organs could not be discerned, owing to poor preservation. The penis (Figure 22B) is similar to other members of *Siphopteron* described in this paper. The prostate is short

with a single convolution. At its anterior end, the prostate gives rise to the penial bulb and the duct of the penial papilla. The penial bulb contains a central fleshy lobe armed with 24 radially arranged hooks. A smaller lateral lobe bears five additional curved spines. The penial duct is short and narrow. It expands into a simple, conical penial papilla that is devoid of armature. The penial papilla and penial bulb merge into the anterior penial sac, which then joins the ciliated sperm groove at the right anterior extreme of the head.

**Discussion:** *Siphopteron flavum* is morphologically similar to other members of the genus. It is unique in that it possesses a terminal rather than lateral flagellum and has penial bulb spines arranged in a large circular whorl with a smaller lateral row of spines.

*Gastropteron bicornutum* Baba & Tokioka, 1965

(Figures 1G, 23, 24)

*Gastropteron bicornutum* BABA & TOKIOKA, 1965:364, text figs. 1–6, pl. 25, figs. 1–9; BABA, 1970:figs. 3–5.

**Distribution:** This species is known only from Japan (BABA & TOKIOKA, 1965) and Papua New Guinea (present study).

**Material:** Two specimens, California Academy of Sciences, San Francisco, CASIZ 066595, W side of Tabat Island, Madang, Papua New Guinea, 10 m depth, on coarse sandy slope, among *Halophila*, 9 February 1988, T. M. Gosliner. One specimen, CASIZ 066596, W side of Pig Island, Madang, Papua New Guinea, 10 m depth, on coarse sandy slope among *Halophila*, 15 February 1988, T. M. Gosliner. One specimen, CASIZ 066597, dissected, W side of Pig Island, Madang, Papua New Guinea, 10 m depth, on coarse sand slope among *Halophila*, 15 February 1988, T. M. Gosliner.

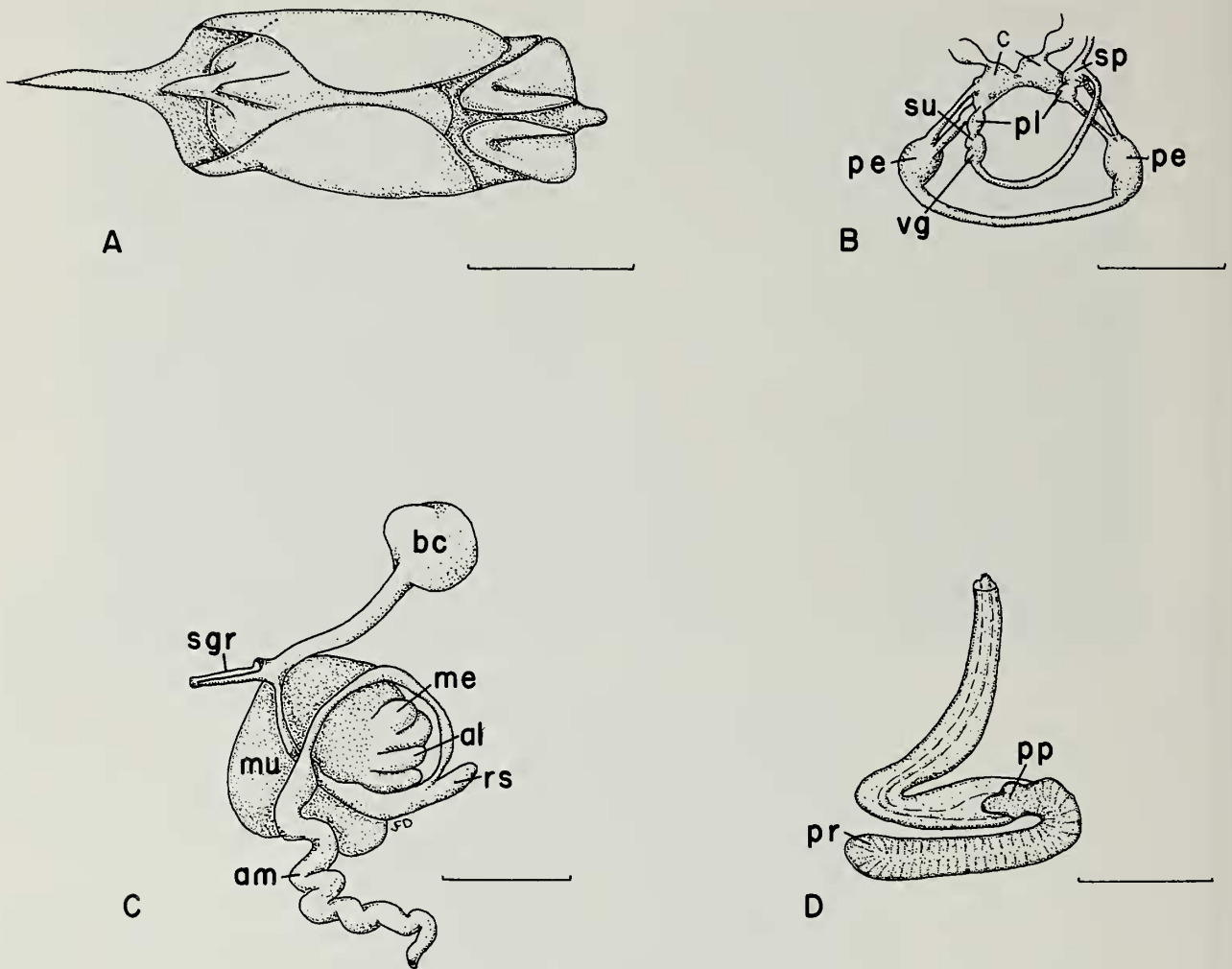


Figure 23

*Gastropteron bicornutum* Baba & Tokioka, 1965. A. Dorsal view of living animal, scale = 2.0 mm. B. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglia; os, osphradial ganglion; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Reproductive system, scale = 1.0 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. D. Penis, scale = 0.5 mm. Key: pp, penial papilla; pr, prostate.

**Natural history:** All four specimens studied here were found near the sea grass, *Halophila* sp., on shallow subtidal sandy slopes. This species closely resembles both an undescribed *Chelidonura* sp. and an undescribed haminoeid, with which it is sympatric. GOSLINER & BEHRENS (1989) have suggested that these three taxa form a Müllerian mimicry complex.

**External morphology:** The four living specimens (Figures 1G, 23A) were 5–7 mm in length. The general body color is translucent white. Black, opaque white, and yellow-orange pigment spots are scattered over the surface of the body in variable densities. This variable pattern makes the animal appear mottled gray or black, depending on

the relative densities of white and black pigments. The head shield (Figure 23A) is broad and triangular. Posteriorly, it terminates in an involuted siphon, which lacks a central ridge. The large and well developed parapodia enable *Gastropteron bicornutum* to swim for extended periods of time. The posterior ends of the parapodia extend just posterior to the hind end of the visceral hump. The visceral hump is oval with a large conical flagellum situated at its posteromedial end. Immediately dorsal to this flagellum is a second, slightly more elongate flagellar process. The ctenidium is large, consisting of 13 primary filaments. The foot is wide for most of its length. Anteriorly, it is bilobed and posteriorly it is tapered with a narrow, elongate "tail." Ventrally, a large pedal gland is present at the posterior end of the foot.

**Digestive system:** Ventral to the large muscular buccal mass is a large oral gland. At the junction of the esophagus with the posterior end of the buccal mass is a pair of large, ventrally directed salivary glands. Within the anterior portion of the buccal mass is a pair of well-developed jaws. These jaws contain numerous, rodlike elements. The radular formula is  $20 \times 4 \cdot 1 \cdot 0 \cdot 1 \cdot 4$  in one specimen examined. The broad inner lateral teeth bear 8–11 elongate denticles on the masticatory margin (Figure 24). The outer laterals are narrow and hook-shaped, with a prominent swelling near their bases.

**Central nervous system (Figure 23B):** The large cerebral ganglia are appressed, with a short commissure separating them. A large swelling of nervous tissue is present at the anterodorsal portion of either cerebral ganglion. Ventral to the cerebral ganglia are the slightly larger pedal ganglia, which are separated from each other by an elongate commissure. Extending posterior from each cerebral ganglia, and joining with the pedal ganglia, is a smaller pleural ganglion. Immediately posterior to the left pleural ganglion, and partially fused with it, is the subintestinal ganglion, followed immediately by the larger visceral ganglion. The visceral loop extends around the posterior portion of the buccal mass, curves anteriorly, and joins the suprainintestinal ganglion adjacent to the osphradial nerve. The suprainintestinal ganglion is situated immediately dorsal to the right pleural ganglion.

**Reproductive system (Figure 23C):** The reproductive anatomy of *Gastropteron bicornutum* is virtually identical to that described for *Sagaminopteron psychedelicum*, with the exception that the shape and relative sizes of the nidamental glands differ slightly. Also, the bursa copulatrix of *G. bicornutum* is more spherical.

The penis (Figure 23D) contains a simple, curved prostate, a short, unarmed, conical papilla, and an elongate duct leading to junction of the penis with the sperm groove.

**Discussion:** *Gastropteron bicornutum* was originally described from eight preserved specimens (BABA & TOKIOKA, 1965). Subsequently, BABA (1970) described the living animal and morphology of the penis. The present material from Papua New Guinea agrees with the previous descriptions in virtually all respects. The specimen described here has a small, but distinct penial papilla, not illustrated by Baba.

*Gastropteron chacmol* Gosliner, sp. nov.

(Figures 1I, 25, 26)

*Gastropteron rubrum*: MARCUS & MARCUS, 1960: *non rubrum* (Rafinesque, 1814); GOSLINER & ARMES, 1984, in part: 60, figs. 19–22, *non rubrum* (Rafinesque, 1814).

**Distribution:** This species was collected from the Yucatan Peninsula of Mexico. Specimens probably attributable to this species have also been collected from Key Biscayne,



Figure 24

*Gastropteron bicornutum* Baba & Tokioka, 1965. Scanning electron micrograph of half-row of radular teeth.

Florida, Grand Cayman Island (MARCUS & MARCUS, 1960; GOSLINER & ARMES, 1984, as *Gastropteron rubrum*, see following discussion), and Caracas Island, Venezuela (Jeff Hamann, pers. comm.).

**Type material:** Holotype, CASIZ 066598, in front of Hotel La Ceiba, Puerto Morelos, Quintana Roo, Mexico, 8 m depth, in mixed sand and *Thalassia*, 4 April 1985, T. M. Gosliner. Twenty-three paratypes, CASIZ 066599, same date and locality as holotype, T. M. Gosliner and M. T. Ghiselin. One paratype, CASIZ 059658, with shell removed, in front of La Ceiba Hotel, Puerto Morelos, Quintana Roo, Mexico, 3 m depth, 27 March 1985, M. T. Ghiselin.

**Natural history:** Specimens of this species have been collected commonly in mixed coarse sand where turtle grass (*Thalassia testudinum* Banks ex König) and a variety of green algae predominate. The animals are competent swimmers and may propel themselves through the water column for extended periods of time.

**Etymology:** A "chacmol" is a reclining figure that is present in several Mayan sites on the Yucatan Peninsula. It is believed that a chacmol served as an altar for offerings of human organs. This species is named after a chacmol because of its geographical proximity to these statues and because of its blood red color.



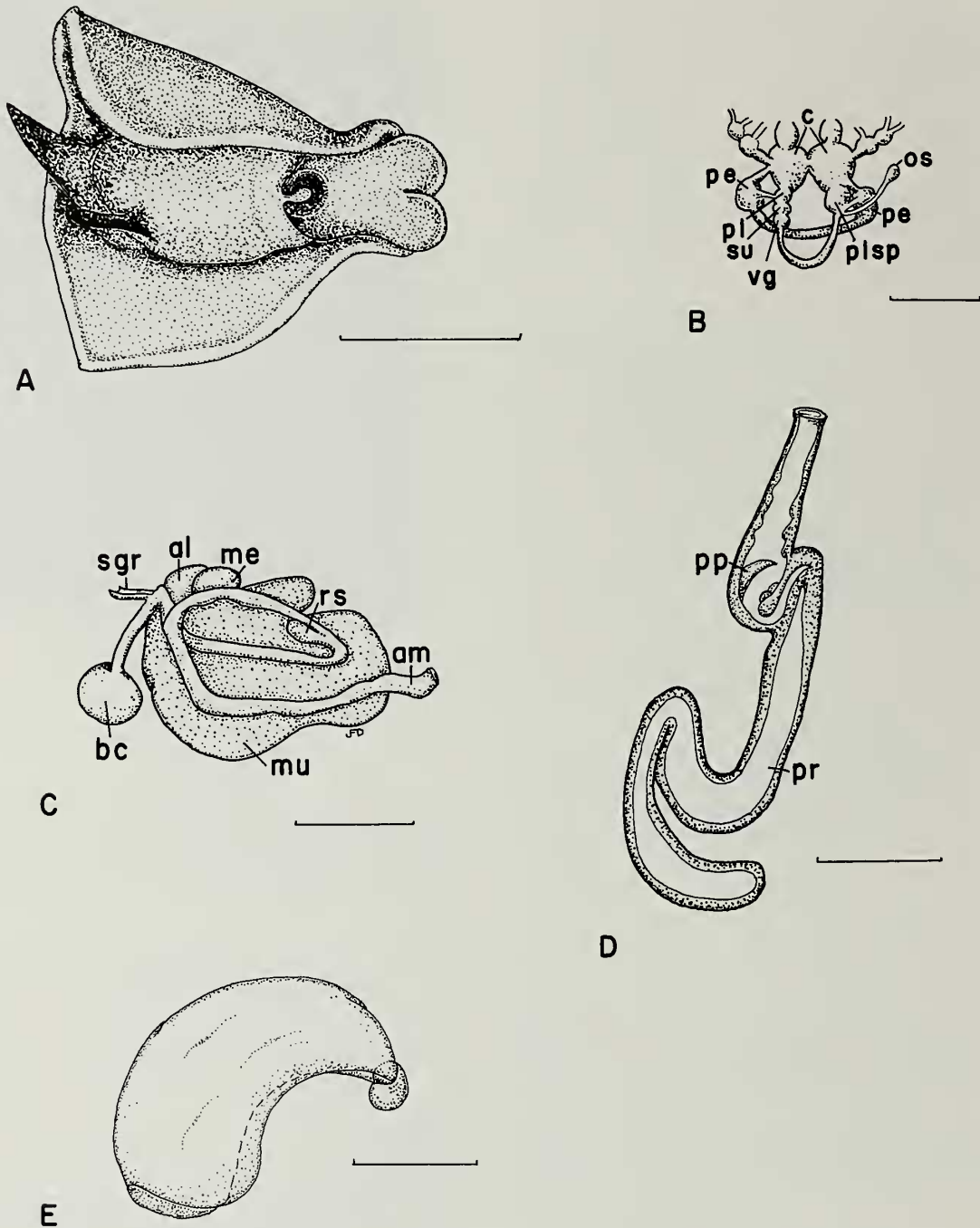


Figure 25

*Gastropteron chacmol* Gosliner, sp. nov. A. Living animal, scale = 2.0 mm. B. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglia; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Reproductive system, scale = 0.5 mm. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; me, membrane gland; mu, mucous gland; rs, receptaculum seminis; sgr, sperm groove. D. Penis, scale = 0.5 mm. Key: pr, prostate. E. Shell, scale = 0.5 mm.

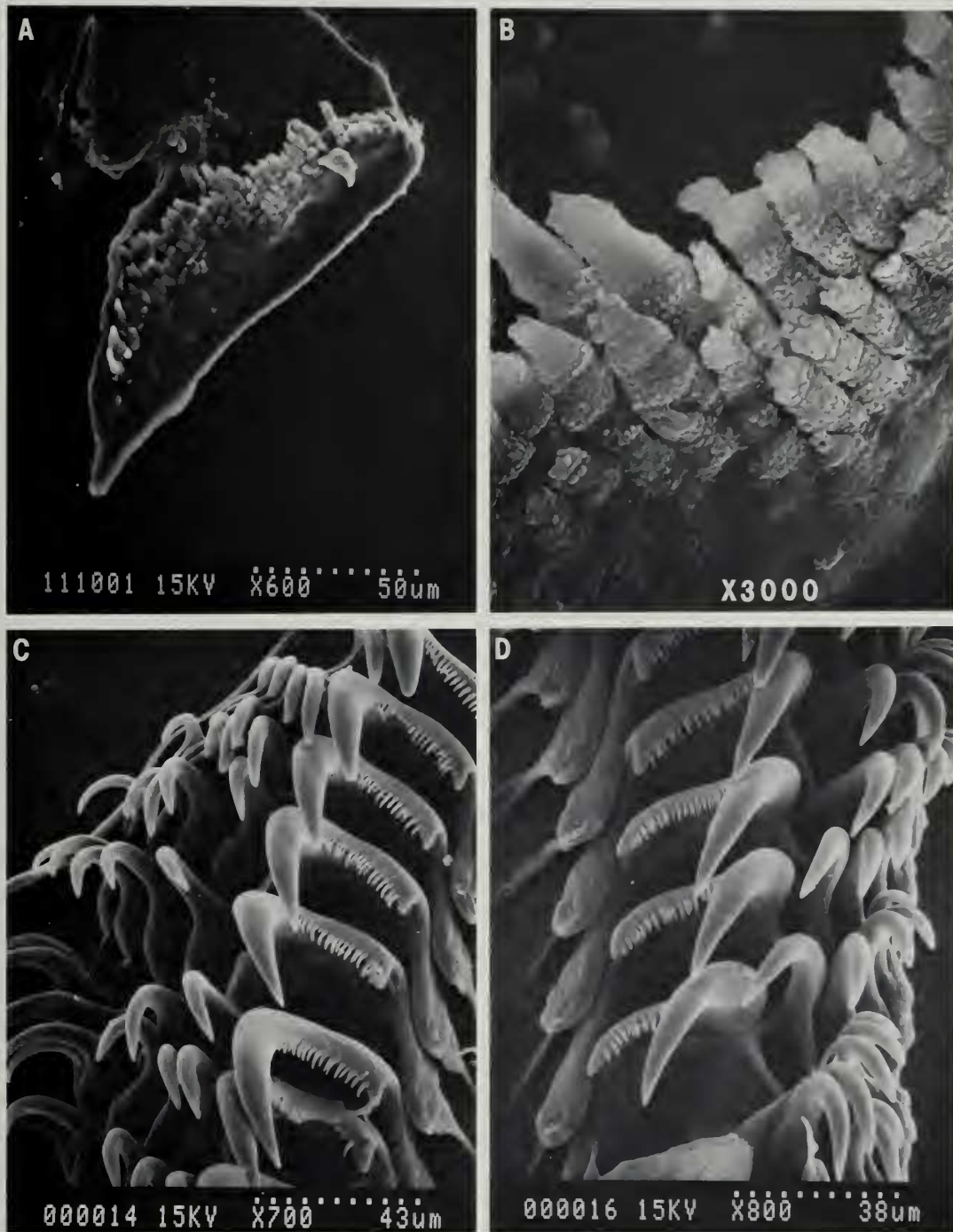


Figure 26

*Gastropteron chacmol* Gosliner, sp. nov. Scanning electron micrographs. A. Entire jaw. B. Jaw elements. C. Half-row of radular teeth. D. Half-row of radular teeth.

**External morphology:** The living animals (Figures 11, 25A) are 3–7 mm in length. The general body color is deep red to plum. Minute yellow spots are scattered over the surface of the body in some specimens. The parapodial

margin is bright yellow. The head shield is rounded and bilobed anteriorly, with a deeply emarginate medial cleft. The head shield tapers posteriorly into an involuted siphonal margin, which lacks a distinct medial crest. The

visceral hump is elongate and ovoid. An elongate filiform flagellum is present on the right side of the body, between the gill and posterior end of the visceral hump. The parapodia are elongate and high, overlapping each other when the animal is at rest. The parapodia are joined to the rest of the body anteriorly and are free for most of their length. There is no distinct separation between the foot and parapodia. The large gill, consisting of 7–10 distinct, simply plicate leaflets, is situated on the right side of the body. A large, ovoid pedal gland is present within the posterior portion of the foot.

**Shell:** The morphology of the shell was studied in one specimen. It consists of a small, calcified embryonic portion and a larger membranous, conchiolin wing (Figure 25E).

**Digestive system:** The buccal mass is large and muscular. A large oral gland is present ventral to the anteriormost portion of the buccal mass. A pair of moderately elongate salivary glands extends posteriorly from the junction of the esophagus with the posterior end of the buccal mass. The anterior end of the buccal mass contains a pair of chitinous jaws (Figure 26A) which are composed of numerous, finely papillate rodlets (Figure 26B). The radular formula is  $17-19 \times 5 \cdot 1 \cdot 0 \cdot 1 \cdot 5$  in three specimens examined. The inner lateral teeth (Figure 26C, D) are broad with a sharp elongate cusp. On the inner margin of the inner lateral teeth is an elongate masticatory margin, bearing 21–24 small, elongate denticles. The edentate outer lateral teeth are progressively shorter and narrower towards the outer margins.

**Central nervous system:** The arrangement of ganglia (Figure 25B) is eutyneurous with a short visceral loop. The large cerebral ganglia are appressed to each other, without a distinct commissure. From their anterior surface arises a slightly smaller concentration of nervous tissue. Laterally and ventrally there are also several swellings and branchings of cerebral nerves. Ventral to the cerebral ganglia are the slightly smaller pedal ganglia, which are connected to each other by a short commissure. Immediately posterior to the left cerebral ganglion are the left pleural, subintestinal, and visceral ganglia. Extending posteriorly from the right cerebral ganglion are the right pleural and suprainestinal ganglia. From the posterior end of the suprainestinal ganglion arise the visceral and osphradial nerves. The visceral nerve joins the visceral ganglion on the other side of the body. The osphradial nerve leads to a small osphradial ganglion.

**Reproductive system:** The arrangement of reproductive organs is monaulic (Figure 25C). The ampulla is straight and narrow. There is no distinct division between the ampulla and the hermaphroditic duct. The hermaphroditic duct passes over the surface of the mucous gland and loops around the albumen and membrane glands. Just before curving back to the genital aperture is a small swelling, the short receptaculum seminis. The hermaphroditic duct

joins the genital aperture at the junction of the nidamental glands and the bursa copulatrix. The thin-walled bursa is connected to the genital aperture by a short stalk.

The penis (Figure 25D) has a thick prostrate with a single convolution. The penis occupies much of the anterior portion of the body. The prostate narrows distally and emerges into the penial sac. The penial sac lacks a distinct papilla but contains a proximally directed, fleshy lobe that is lined by chitin. The penial aperture joins the anterior end of the sperm groove on the right side of the head.

**Egg mass:** The egg mass is a gelatinous sphere that is attached to the substrate by means of a mucus thread. Within this gelatinous mass are numerous individually encapsulated yellow eggs.

**Discussion:** *Gastropteron chacmol* most closely resembles *G. rubrum* (Rafinesque, 1814) and *G. vespertilium* Gosliner & Armes, 1984, in aspects of its coloration, external anatomy, and internal anatomy (Table 1). These three species have an elongate flagellum on the right side of the body and inner lateral teeth bearing numerous small denticles. All three species differ in their coloration. The ground color of *G. vespertilium* is grayish or purplish black with occasional blue-gray spots on the parapodia. Yellow, or more rarely green or blue, lines are present on the margins of the siphon and parapodia. The flagellum is translucent white. The ground color of *G. rubrum* is pale red with scattered white or yellow spots and pale yellow or bluish white lines on the parapodial and siphonal margins (SALVINI-PLAWEN & ABBOTT, 1974; Malcolm Edmunds, pers. comm.). Though *G. chacmol* is also reddish in color, the red is deeper and richer, and the parapodial margin is a bright yellow. The siphon and flagellum are the same color as the ground color, without any additional pigment.

*Gastropteron chacmol* is most similar to *G. vespertilium* in external morphology. Both are small in size (a maximum of 5–7 mm in length), have a distinctly bilobed anterior margin of the head, and have a gill composed of 10 or fewer leaflets. In contrast, *G. rubrum* is large (up to 30 mm in length), has an undivided head, and has a large gill composed of 23–30 leaflets.

Internally, differences also separate the three species. The radula in the three species is very similar in formula and shape and number of teeth. The radular teeth of *Gastropteron rubrum* are larger, but are thin and flimsy. The denticles on the masticatory margin of the inner lateral teeth are weakly developed.

The cerebral ganglia of *Gastropteron chacmol* are appressed to each other, without a distinct commissure, while both *G. rubrum* and *G. vespertilium* have a commissure that at least equals the diameter of the ganglia.

The most profound differences between *Gastropteron chacmol*, *G. rubrum*, and *G. vespertilium* are in the structure of the penis. Both *G. chacmol* and *G. vespertilium* have a short, indistinct penial papilla, whereas that of *G. rubrum* is elongate and conical. The prostate of *G. chacmol*



Table 1  
Morphological variation in three *Gastropteron* species.

Species	Color	Length	Gills	Radula	Cerebral commissure	Penial papilla	Prostate
<i>Gastropteron rubrum</i>	pale reddish with white spots, white or yellow parapodial & siphonal lines	10–26 mm	23–30	20–40 × 5·1·0·1·5	present	elongate	highly convoluted
<i>Gastropteron vespertilium</i>	grayish black with blue-gray spots, yellow, blue, or green parapodial & siphonal lines	3–5 mm	9–10	15–21 × 5–6·1·0·1·5–6	present	short	1 convolution
<i>Gastropteron chacmol</i>	deep red to plum, yellow or blue parapodial line	3–7 mm	7–11	16–19 × 5·1·0·1·5	absent	short	1 convolution

and *G. vespertilium* is thick, consisting of only one or two convolutions, whereas that of *G. rubrum* is thin and highly convoluted (GOSLINER & ARMES, 1984). In addition, *G. vespertilium* possesses a separate spermatic bulb, which is absent in the other two species.

In the description of *Gastropteron vespertilium*, GOSLINER & ARMES (1984) reviewed the morphology of *G. rubrum*, based on the pertinent literature and examination of Mediterranean and eastern and western Atlantic material. The western Atlantic specimens had fewer gill lamellae and were smaller in length. Differences between eastern and western Atlantic individuals were attributed to smaller size and immaturity of the western Atlantic material. However, the discovery of mature individuals of *G. chacmol* ranging from 3 to 7 mm has necessitated the re-examination and more critical comparison of specimens of *G. rubrum* studied by Gosliner and Armes. The holotype of *G. rubrum manx* Marcus & Marcus, 1966, from West Africa, together with specimens from Palermo, Italy, agrees completely with the description by GOSLINER & ARMES (1984:figs. 24, 25) and previous accounts of *G. rubrum* from the Mediterranean (VAYSSIÈRE, 1880, 1885; BERGH, 1893; GUIART, 1901). On the other hand, the two western Atlantic specimens from Florida (USNM 836667) and Grand Cayman Island (CASIZ 034121) have a slightly convoluted prostate without an elongate penial papilla. The remainder of their morphology is identical to that of *G. chacmol*. Therefore, all published records of *G. rubrum* in the western Atlantic likely refer to *G. chacmol* rather than to *G. rubrum*.

*Gastropteron hamanni* Gosliner, sp. nov.

(Figures 1H, 27, 28)

**Distribution:** This species is known only from the type locality in the Turks and Caicos Islands.

**Type material:** Holotype, CASIZ 066603, Sellars Cut, Providenciales Island, Caicos Islands, Turks and Caicos, 20 m depth, Jeff Hamann.

**Etymology:** *Gastropteron hamanni* is named for Jeff Hamann, who collected the only known specimen of this species. Jeff is a good friend and has been an enthusiastic and generous supporter of opisthobranch research for many years.

**External morphology:** The living animal (Figure 1H) was 4 mm in length. The ground color is uniformly yellow with a maroon apex to the siphon. The head shield is roughly triangular, broadest anteriorly. It is relatively short, comprising only about one-fourth of the body length. Its posterior end forms an involuted siphon, which lacks a distinct medial crest. The parapodia are elongate and high, overlapping each other when the animal is actively crawling. The visceral hump is elongate and ovoid, without any flagellum or other appendages. The gill is small, consisting of 2 or 3 indistinct leaflets. The foot is not distinctly separated from the parapodia. A large pedal gland is present at the posterior end of the foot.

**Digestive system:** The buccal mass (Figure 27A) is short and muscular. A pair of large, ventrally directed salivary glands is present at the junction of the esophagus with the posterior end of the buccal mass. The salivary glands are two to three times the length of the buccal mass. Within the buccal mass is a thin, chitinous lining. No distinct jaws with rodlets were observed. A small radula was present. Its formula was  $12 \times 3 \cdot 1 \cdot 0 \cdot 1 \cdot 3$ . The inner lateral teeth (Figure 28A, B) are broadly triangular, narrow in the outer portion. There are approximately eight short, indistinct denticles on the sloping masticatory border. The outer lateral teeth are thin and simply hook-shaped, with only a single cusp.

**Central nervous system:** The arrangement of the ganglia (Figure 27B) is euhyneurous. The cerebral ganglia are large and appressed to each other, without a distinct commissure. The pedal ganglia are approximately the same size as the cerebrals and are connected to each other by an elongate commissure. Immediately posterior to the left

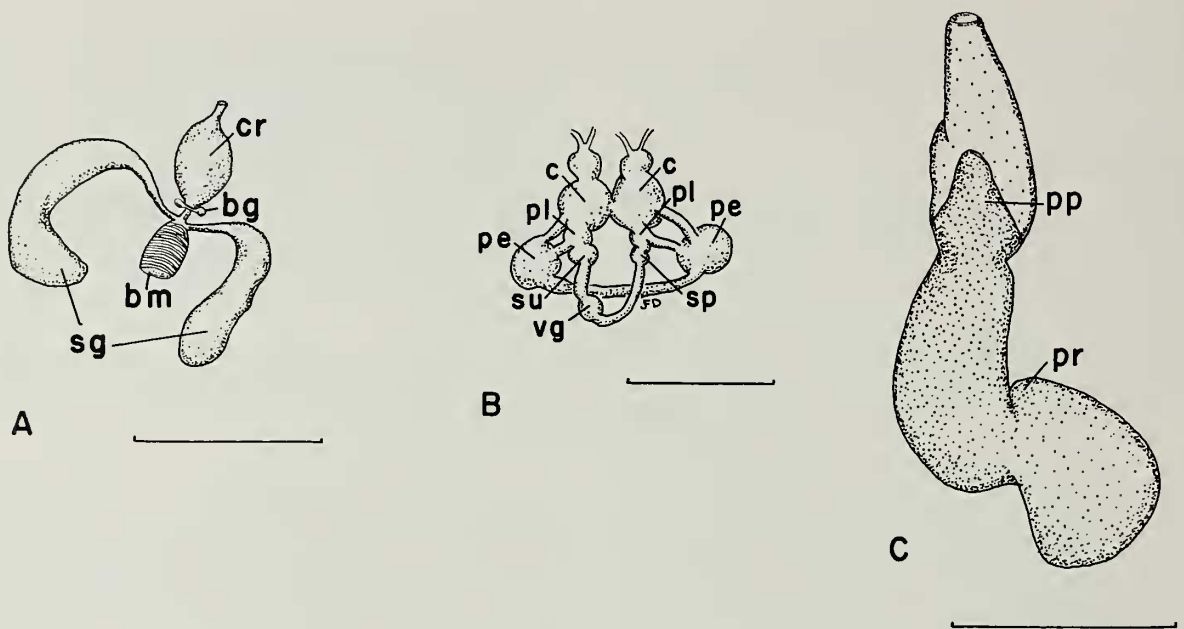


Figure 27

*Gastropteron hamanni* Gosliner, sp. nov. A. Buccal mass, scale = 1.0 mm. Key: bg, buccal ganglia; bm, buccal mass; cr, crop; sg, salivary gland. B. Central nervous system, scale = 0.5 mm. Key: c, cerebral ganglion; pe, pedal ganglion; pl, pleural ganglion; sp, suprainintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. C. Penis, scale = 0.2 mm. Key: pp, penial papilla; pr, prostate.

cerebral ganglion are the left pleural and subintestinal ganglia. After a moderate distance there is a small visceral ganglion. The visceral loop curves behind the esophagus and joins the suprainintestinal ganglion on the right side of the body. Immediately anterior to the suprainintestinal ganglion is the right pleural ganglion.

**Reproductive system:** Details of the posterior genital complex could not be ascertained owing to poor preservation. The penis (Figure 27C) is simple with a short, slightly curved prostate, which joins a short penial sac. No distinct papilla is in the sac.

**Discussion:** In its coloration *Gastropteron hamanni* most closely resembles *Siphopteron flavum* (Tokiooka & Baba, 1964). However, *G. hamanni* lacks dark pigment on the posterior end of the visceral hump. It also lacks the medial siphonal crest and distinctive posterior extension of the visceral hump that characterize *S. flavum* (Tokiooka & Baba, 1964; Carlson & Hoff, 1974; Bertsch & Johnson, 1981). The radular morphology of the two species appears similar except that *S. flavum* appears to have a more extensive masticatory margin than in *G. hamanni*.

The most significant differences between the two species are in the structure of the penis. *Gastropteron hamanni* has a simple unarmed penis, whereas *Siphopteron flavum* has a distinct penial bulb containing two series of curved hooks and a separate penial duct and papilla.

*Gastropteron odhneri* Gosliner, sp. nov.

(Figures 29, 30)

**Distribution:** This species is known only from the type locality, Bonin Island, Japan.

**Type material:** Holotype, Naturhistoriska Riksmuseet, Stockholm, Dr. Sixten Bocks' Japan Expedition 1914, off Chichijima, Bonin Islands (Ogasawara), Japan, 70 fathoms (ca. 128 m) depth, 8 July 1914, S. Bocks.

Paratypes, five specimens. Naturhistoriska Riksmuseet, Stockholm No. 1288, same locality and date as holotype.

**Etymology:** This species is named after the late Dr. Nils Hjalmar Odhner, who contributed greatly to our understanding of opisthobranch systematics and evolution. Dr. Odhner first indicated that these specimens represented an undescribed species.

**External morphology:** The preserved specimens (Figure 29A, B) are 4–5.5 mm in length. The head shield is bilobed anteromedially and is roughly triangular. There is no distinct siphonal crest at its posterior limit, only a short posterior lobe. The parapodia are broad, extending for most of the length of the animal. The visceral hump is ovoid. On its right side is a curved ridge that partially covers the ctenidium. At the posterior limit of the visceral hump is a curved, triangular flagellum. The ctenidium is composed

of 3–5 pinnate leaflets. The anus is situated immediately posterior to the gill. The foot (Figure 29B) is distinct from the parapodia and is widest posteriorly. An ovoid pedal gland is present in the posterior third of the foot. It has an elongate slit extending posteromedially from the glandular body to the posterior limit of the foot.

**Shell:** Although the shell was entirely dissolved in all material, a large curved conchiolin membrane remained, indicating that *Gastropteron odhneri* likely possesses a large, calcified shell.

**Digestive system:** The buccal mass is large and muscular, occupying much of the region of the head shield. At the junction of the esophagus with the posterodorsal end of the buccal mass is a pair of elongate, tubular salivary glands. The esophagus is elongate and glandular and joins the stomach within the large digestive gland. Numerous foraminiferans were contained within the stomach of one specimen. There is a large labial cuticle, bearing rows of distinct jaw platelets (Figure 30A), which are restricted to two small areas on the medial portion of its anterodorsal margin. The radular formula in one specimen was  $23 \times 6 \cdot 1 \cdot 0 \cdot 1 \cdot 6$ . The inner lateral teeth (Figure 30B, C) are broad with a longer inner limb. A large, curved primary cusp with 9–12 irregular denticles is on the masticatory margin on the inside of the cusp. The denticles become decreasingly distinct towards the inner edge of the tooth. On the innermost portion of the masticatory margin is a thickened triangular area. The outer lateral teeth have a single hook-shaped cusp and decrease in size towards the outer limit of the radula.

**Central nervous system:** The arrangement of ganglia (Figure 29C) is euryneurous, with a short visceral loop. The cerebral ganglia are large and are separated by a short, but distinct commissure. Additional ganglionic tissue is situated anterodorsally to each cerebral ganglion. The pedal ganglia are situated ventrally to the rest of the nerve ring and are joined to the cerebral ganglia by long connectives and to the pleural ganglia by shorter ones. The pedal ganglia are connected to each other by an even longer connective. The pleural ganglia are separated from the cerebrals by a short connective. The subintestinal and visceral ganglia are immediately posterior to the left pleural ganglion. A curved visceral loop separates the visceral ganglion from the suprainintestinal ganglion, which is connected directly to the right pleural ganglion.

**Reproductive system:** The posterior reproductive system was not mature, with only a small aggregation of reproductive cells. These cells are not clearly differentiated into reproductive organs.

The penis (Figure 29D) is fully developed in the two specimens examined. A short, curved prostate gland empties into an expanded penial sac, which contains several lobes of the penis. A retractor muscle is connected to the penis near the junction of the prostate with the penial sac.



Figure 28

*Gastropteron hamanni* Gosliner, sp. nov. A. and B. Scanning electron micrographs of inner lateral teeth.

The primary penial papilla is laterally directed, indented apically, but devoid of any armature. A long duct of the penis sac joins the ciliated sperm groove on the right side of the head.



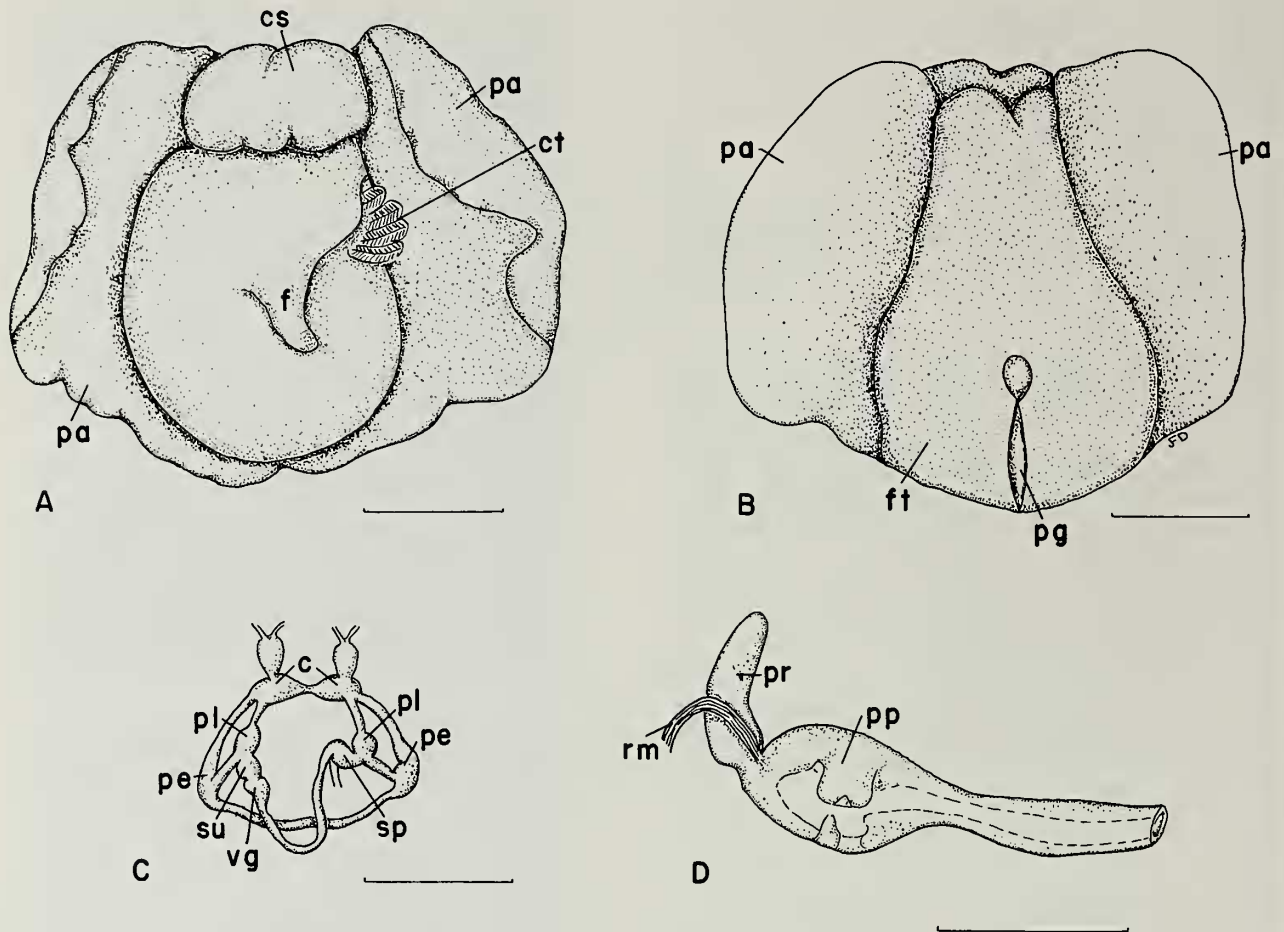


Figure 29

*Gastropteron odhneri* Gosliner, sp. nov. A. Dorsal view of preserved animal, scale = 1.0 mm. Key: cs, cephalic shield; ct, ctenidium; f, flagellum; pa, parapodium. B. Ventral view of preserved animal, scale = 1.0 mm. Key: ft, foot; pa, parapodium; pg, pedal gland. C. Central nervous system, scale = 1.0 mm. Key: c, cerebral ganglia; pe, pedal ganglion; pl, pleural ganglion; sp, supraintestinal ganglion; su, subintestinal ganglion; vg, visceral ganglion. D. Penis, scale = 0.5 mm. Key: pp, penial papilla; pr, prostate; rm, retractor muscle.

**Discussion:** *Gastropteron odhneri* is similar to *G. rubrum* (Rafinesque, 1814), *G. pacificum* Bergh, 1893, *G. sibogae* Bergh, 1905, and *G. japonicum* Tokioka & Baba, 1964, in possessing a large, rounded visceral hump and pinnate, dorsally directed pinnae of the ctenidium. *G. odhneri* differs from all other members of the genus in having the foot widest posteriorly rather than anteriorly, and in having only 3–5 gill pinnae. All other species have 12–22 leaflets. The jaws of *G. odhneri* are restricted to a very small portion of the dorsal labial cuticle, whereas in other species they are more widespread. *Gastropteron odhneri* is the only species in the genus with the denticles on the inner lateral teeth becoming less distinct towards the inner margin. The penial morphology is also unique, with a short curved prostate and a lobed, laterally directed papilla.

*Gastropteron* sp.

(Figure 31)

**Material:** One specimen, California Academy of Sciences, San Francisco, CASIZ 066604, Easter Island, Louis de Salvo.

**External morphology:** The preserved specimen was 2 mm in length. The head shield is roughly triangular with no distinct siphon or siphonal crest. The parapodia are short, not overlapping. The visceral hump is ovoid, and bears a short, simple flagellum on its right side. The gill is small with only a few pinnae.

**Shell:** A calcified shell is present but, owing to fragmentation, its shape cannot be described.

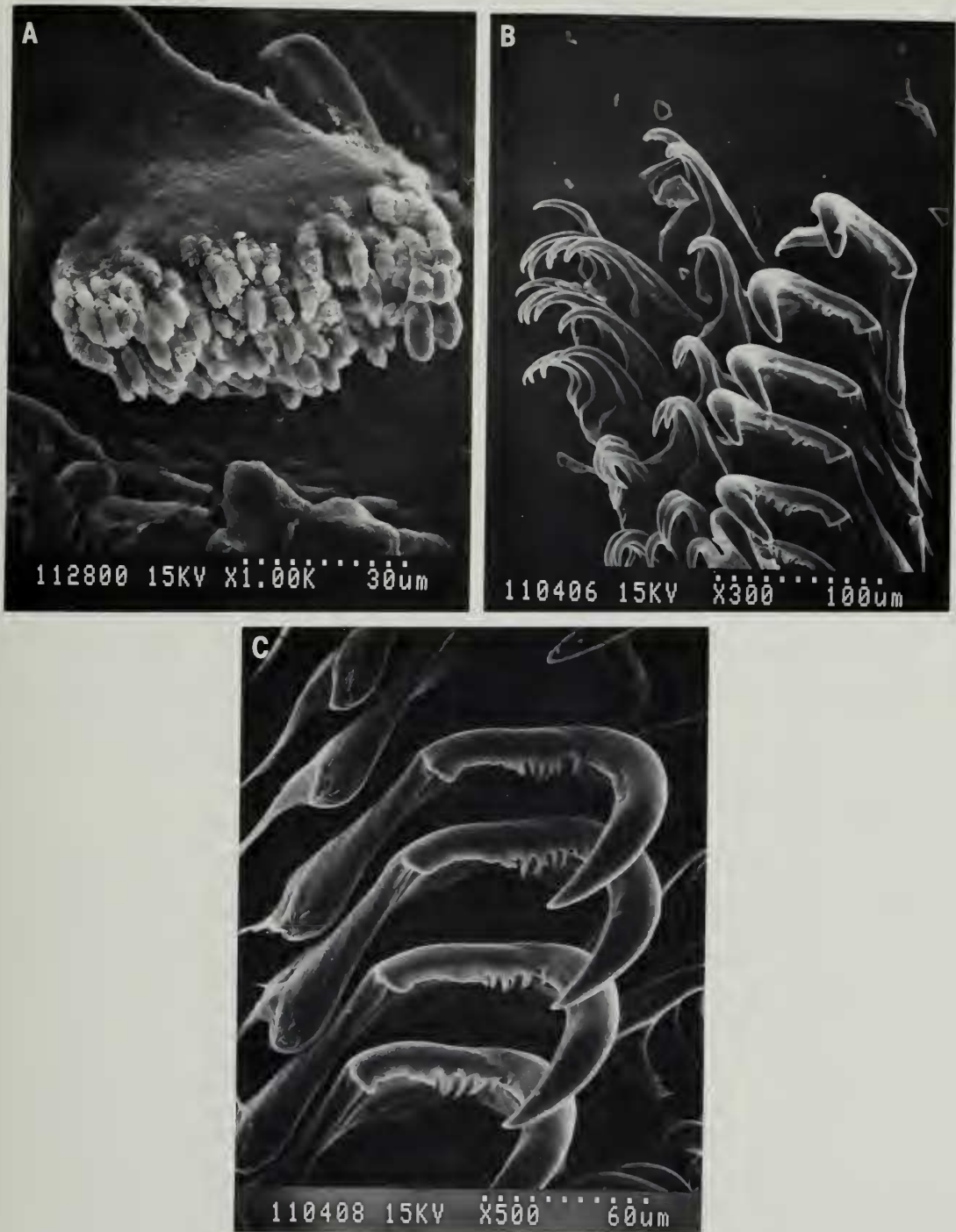


Figure 30

*Gastropteron odhneri* Gosliner, sp. nov. Scanning electron micrographs. A. Jaw platelets. B. Half-row of radular teeth. C. Inner lateral teeth.

**Digestive system:** The buccal mass is short and muscular. The labial cuticle is thin, and apparently devoid of distinct jaw plates. The radular formula is  $18 \times 2.1 \cdot 0.1 \cdot 2$ . The inner lateral teeth (Figure 31) are broad with an elongate

inner limb. A large curved cusp is on the outer edge of the inner lateral. There are 6–9 evenly spaced denticles on the masticatory border. The innermost portion of the masticatory border bears an elongate, triangular cusp. The two



Figure 31

*Gastropteron* sp., Easter Island. Scanning electron micrograph of half-row of radular teeth.

outer lateral teeth are simple hook-shaped, with the inner one being slightly larger than the outer.

**Reproductive system:** Details of the posterior reproductive system could not be determined owing to poor preservation. The penis has a short, straight prostate with a simple, conical, unarmed penial papilla.

**Discussion:** Based on its morphology, with a narrow radula containing only two outer laterals per side, this species appears to be undescribed. However, because only one specimen was collected, without any description of the living animal, it is preferable not to describe it until more material becomes available.

## DISCUSSION

Until recently, the Gastropteridae appeared to be a relatively small and morphologically uniform taxon. Members of the family were known largely from temperate waters. TOKIOKA & BABA (1964), BABA & TOKIOKA (1965), and MINICHEV (1967) described several additional taxa from Japan and China, including the distinct genera *Sagaminopteron* and *Enotepteron*. More recently, CARLSON & HOFF (1973, 1974) and HOFF & CARLSON (1983) described an additional seven species from the tropical western Pacific. GOSLINER (1984, 1988a), GOSLINER & ARMES (1984), and GOSLINER & WILLIAMS (1988) have added five new species

from the southeastern Atlantic, western Atlantic, and western Indian Ocean.

Most of the recently described species inhabit the Indo-Pacific tropics and exhibit considerably more morphological variability than previously believed to occur within the Gastropteridae (Table 2). Table 3 provides the key to each character state for the characters considered.

## Character Polarity

In order to discuss the phylogenetic relevance of this variability, it is first necessary to establish the polarity of each character. Members of the Gastropteridae are highly derived cephalaspideans, compared with other members of the Philinacea (RUDMAN, 1978; GOSLINER, 1980, 1981), and possess several autapomorphic features, such as a posterior pedal gland with a longitudinal slit. This fact makes it difficult to determine polarity within the Gastropteridae solely by means of outgroup comparison. For this reason, other criteria such as ontogenetic data or functional arguments are sometimes invoked to supplement outgroup comparison. The numbering system for characters, from 1 to 24, is reiterated in Tables 2 and 3.

**1. Shell:** Some character polarities can be determined with relative confidence. Loss of the shell in post-metamorphic juveniles and adults is a common apomorphic feature throughout the Opisthobranchia (GOSLINER & GHISELIN, 1984; GOSLINER, 1988b). The polarity of shell loss is not only supported by outgroup comparison, but by ontogenetic data, where virtually all opisthobranch larvae possess a shell.

**2. Siphon:** The presence of a siphon at the posterior end of the cephalic shield is an autapomorphy for the family. Presumably the siphon functions as a chemosensory organ analogous to the rhinophores of other opisthobranchs. Because it is absent in other taxa, outgroup comparison provides no information about the polarity of the variation observed in the morphology of the siphon within the Gastropteridae. However, functional arguments, as advocated by GOSLINER & GHISELIN (1984), suggest that the elaboration of a medial crest within the siphon provides greater surface area for sensory detection and increases the structural integrity of the siphon. Therefore, the presence of a siphon is considered to represent the apomorphic state.

**3. Flagellum:** The flagellum, located near the posterior end of the visceral hump, may be homologous to the pallial caecum of other cephalaspideans (e.g., *Acteon* and *Scaphander*). Its position on the right side of the body, posterior to the gill, is similar to that of the pallial caecum. If these structures are indeed homologous, the presence of a flagellum would represent the plesiomorphic state within the Gastropteridae. If the pallial caecum and flagellum are not homologous, the flagellum is autapomorphic within the Gastropteridae. Subsequent cladistic analysis indicates that a flagellum is absent in different lineages of opo-



Table 2  
Morphological variation in the Gastropteridae.

Species	Shell	Siphonal crest	Flagellum reduction	Flagellum addition	Gill	Spheres	Tail	Jaws	Outer laterals	Inner lateral	Cerebral commissure	Visceral ganglion	Spermatheca bulb	Penial papilla	Penial duct	Penial bulb	Penial spines I	Penial spines II	Swimming	Notched foot	Color	Pigmented border	Pigmented siphon	Convolved prostrate
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>rubrum</i>	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1
<i>vespertilium</i>	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1
<b><i>chacmol</i></b>	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1
<b><i>hamanni</i></b>	9	0	1	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	9	0	1	0	1	0
<i>japonicum</i>	0	0	1	0	1	0	0	0	1	1	9	9	9	9	9	9	9	9	9	0	0	0	0	9
<i>bicornutum</i>	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	9
<i>sibogae</i>	0	0	0	0	9	0	0	0	1	5	0	9	9	9	9	9	9	9	9	9	9	9	9	9
<i>pacificum</i>	0	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>viride</i>	9	0	1	1	1	0	0	2	1	1	9	9	9	9	9	9	9	9	0	0	1	1	0	9
<b><i>odhneri</i></b>	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	9	0	9	9	9	0
sp., Easter Island	0	0	0	0	0	0	0	2	1	1	1	9	0	0	0	0	0	0	9	0	9	9	9	0
<i>E. flavum</i>	1	0	0	0	0	2	0	0	1	2	1	1	0	2	0	0	0	0	9	0	9	9	9	0
<i>rosevaleri</i>	1	0	0	0	0	1	0	2	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>ornatum</i>	9	1	0	2	2	0	0	2	0	3	9	9	9	9	9	9	9	9	0	1	1	0	1	9
<i>nigropunctatum</i>	0	1	0	0	2	0	0	2	0	3	1	0	0	0	0	0	0	0	0	1	3	0	1	0
<i>bilealbum</i>	0	1	0	0	2	0	0	2	0	3	1	0	0	0	0	0	0	0	0	1	1	0	1	0
<i>psychedelicum</i>	0	1	0	0	2	0	0	0	0	3	1	0	0	0	0	0	0	0	0	1	1	0	1	0
<i>fuscum</i>	1	1	0	0	0	0	0	9	9	9	9	9	9	9	9	9	9	9	9	0	1	1	1	9
<i>polinpei</i>	1	1	1	0	0	0	0	2	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0
<i>ladrones</i>	1	1	0	0	0	0	0	2	0	0	1	1	0	0	1	1	1	0	0	0	1	0	1	0
<i>S. flavum</i>	1	1	1	1	0	0	0	2	0	0	1	0	0	0	1	1	2	0	0	0	2	0	2	0
<i>brunneomarginatum</i>	1	1	0	0	0	0	0	2	0	0	1	0	0	0	1	1	0	0	1	0	2	1	2	0
<i>citrinum</i>	1	1	0	0	0	0	0	2	0	0	1	0	0	0	1	1	0	0	0	0	2	0	2	0
<b><i>nigromarginatum</i></b>	1	1	0	0	0	0	0	2	0	0	1	0	0	0	1	1	2	0	0	0	2	1	2	0
<i>michaeli</i>	9	1	1	0	0	0	0	2	0	0	1	0	0	0	1	1	2	0	0	0	2	0	2	0
<b><i>tigrinum</i></b>	1	1	0	0	0	0	0	2	0	0	1	0	0	0	1	1	2	0	1	0	2	0	2	0
<b><i>quadrispinosum</i></b>	1	1	0	0	0	0	0	0	2	3	1	0	0	0	1	1	1	1	0	0	1	0	1	0
<i>flavobrunneum</i>	0	1	1	0	0	0	0	2	2	4	0	0	1	3	0	0	0	0	0	0	1	0	0	0
<i>albovarantium</i>	0	1	1	0	0	0	0	2	2	4	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Character number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24

0 = ancestral; 1-5 = derived states; 9 = missing data.

Table 3  
Coding schemes for characters in Table 2.

1. Shell	0 = present	1 = absent	
2. Siphonal crest	0 = absent	1 = present	
3. Flagellum	0 = present	1 = absent	
4. Secondary flagellum	0 = absent	1 = single	2 = multiple
5. Gill	0 = simple	1 = bipinnate	2 = multiple or tripinnate
6. Spheres	0 = absent	1 = sessile	2 = stalked
7. Tail	0 = absent	1 = present	
8. Jaws	0 = well developed	1 = reduced	2 = absent
9. Outer laterals	0 = multiple	1, 2 = reduced number	
10. Inner laterals	0 = simple, denticulate	1 = triangular denticles	2 = few large denticles
	3 = 2 triangular denticles	4, 5 = denticles absent	
11. Cerebral commissure	0 = long	1 = short	
12. Visceral ganglion	0 = distinct	1 = fused	
13. Spermatic bulb	0 = absent	1 = present	
14. Penial papilla	0 = simple	1 = papillate	2 = absent
	3 = apical ring		
15. Penial duct	0 = absent	1 = present	
16. Penial bulb	0 = absent	1 = present	
17. Penial spines I	0 = absent	1 = longitudinal rows	2 = transverse rows
18. Penial spines II	0 = absent	1 = present	
19. Swimming	0 = capable	1 = incapable	
20. Foot	0 = simple	1 = notched	
21. Color	0 = cryptic	1 = aposematic	2 = yellow or orange aposematic
	3 = special resemblance		
22. Pigmented border	0 = absent	1 = present	
23. Pigmented siphon	0 = same color as body	1 = different	2 = brown or black
24. Prostrate	0 = simple	1 = convoluted	

morphic Gastropteridae, further suggesting that its absence represents the derived state.

The flagellum, in most species, is a simple appendage located on the right side of the body. In *Siphopteron flavum* and *Gastropteron viride* the flagellum is terminal on the posterior end of the visceral hump. These elaborations appear to represent derivations from the ancestral condition. The flagellum is entirely absent in seven species of Gastropteridae (Table 2). This loss has apparently occurred polyphyletically on several occasions within the Gastropteridae.

BURN (1980) speculated that the flagellum has evolved as an accessory copulatory structure, and is related to the presence of penial spines in some members of the family. However, a flagellum is present in many species that lack penial spines. Conversely, at least one species with penial spines, *Siphopteron michaeli*, entirely lacks a flagellum. *Gastropteron chacmol* and *S. quadrispinosum* have been observed copulating and do not use the flagellum in the process of mating.

**4. Additional flagellar appendages:** In some species of Gastropteridae the primary flagellum is present, but additional appendages are also present on the posterior portion of the visceral hump. In *Gastropteron bicornutum* a second appendage is present ventral to the primary flagellum. In *Sagaminopteron ornatum* a series of four protuberances is present on the posterior end of the body.

These are considered to represent apomorphies within the family.

**5. Ctenidium:** The ctenidium is simply plicate in virtually all primitive opisthobranchs and is considered here also to represent the plesiomorphic condition in the Gastropteridae. In several more-derived species of *Gastropteron*, the ctenidium has become enlarged and bipinnate. In the case of *Sagaminopteron*, there may be two or more distinct gills. These elaborations, generally present in the larger members of the family, are probably a result of increased respiratory demands.

**6. Spheres:** In species of *Enotepteron*, the posterior edge of the parapodia bears a pair of spherical appendages. In *E. rosewateri* these are sessile, whereas in *E. flavum* they are stalked. The presence of these structures is considered to be apomorphic within these taxa and stalked appendages appear to be derived from sessile ones, based on their more complex structure. BURN (1980) suggested that these structures have evolved for grasping during copulation. This is unlikely, because neither species has copulatory spines and *E. flavum* entirely lacks a penial papilla (MINICHEV, 1967). The function of these structures remains unknown.

**7. Posterior end of foot:** In virtually all cephalaspideans, the posterior end of the foot is short and rounded. This is also the case in most species of Gastropteridae. However, in *Gastropteron bicornutum* the tail possesses an elongate,

filiform extension. This appears to be a derived feature that enhances the resemblance between this species, an undescribed haminoeid, and an undescribed species of *Chelidonura*, all of which are sympatric in Papua New Guinea (GOSLINER & BEHRENS, 1989, in press).

**8. Jaws:** The presence of a pair of jaws bearing chitinous rodlets is widespread throughout cephalaspidean opisthobranchs and is considered to represent the plesiomorphic state within the subclass (GOSLINER, 1980, 1988b). Jaws are reduced in *Gastropteron odhneri* and absent in many representatives of the Gastropteridae. In the latter cases, only a thin chitinous lining of the buccal mass remains.

**9. Outer lateral teeth:** Within the cephalaspidean opisthobranchs it is difficult to establish a plesiomorphic radular configuration, owing to extreme variability among primitive members of the clade. However, within the more ancestral Philinacea the plesiomorphic state is well established. RUDMAN (1978) and GOSLINER (1980) have suggested that a larger number of outer lateral teeth per radular row represents the ancestral configuration. This polarity also applies within the Gastropteridae. Species of *Sagaminopteron* have the broadest radulae within the family, and reduction in the number of teeth per row has evolved independently in other members of the family.

**10. Inner lateral teeth:** Members of the Philinacea are characterized by having a pair of broad inner lateral teeth, each bearing numerous small denticles along its masticatory border (RUDMAN, 1972, 1978; GOSLINER, 1980). This is considered to represent the ancestral condition within the Gastropteridae. In other members of the family, there may be a reduction in the number of denticles. In some cases this appears to involve fusion of denticles to form fewer, larger ones. The most extreme cases involve the loss of all denticles, leaving a smooth masticatory margin. In species of *Gastropteron* there is a triangular thickening on the inner edge of the masticatory border. This structure is not present in any other philinaceans, and is considered to be apomorphic within these Gastropteridae.

**11. Cerebral commissure:** In virtually all plesiomorphic opisthobranchs the cerebral ganglia are well separated from each other by a commissure that is approximately equal in length to the diameter of the cerebral ganglion. This configuration is also present in some species of *Gastropteron* (GOSLINER & ARMES, 1984), and is considered to represent the plesiomorphic condition for the family. However, in most members of the Gastropteridae the cerebral ganglia are appressed to each other and no distinct commissure is present.

**12. Visceral and subintestinal ganglia:** In plesiomorphic cephalaspidean opisthobranchs, all of the major ganglia are well separated from each other (GOSLINER, 1981). The visceral and subintestinal ganglia are distinct in most plesiomorphic opisthobranchs, including most members of the

philinacean families Aglajidae (RUDMAN, 1974; GOSLINER, 1980) and Philinidae (RUDMAN, 1972; GOSLINER, 1988b). On this basis, distinct visceral and subintestinal ganglia are also considered plesiomorphic within the Gastropteridae and their fusion represents the derived condition.

**13. Spermatic bulb:** With the exception of members of the Acteonacea and one species of *Ringicula*, all cephalaspideans have an open, ciliated sperm groove leading to a cephalic penis. The penis in most cephalaspideans has a simple prostate. In some taxa, such as in many species of *Runcina* (GHISELIN, 1963; KRESS, 1977), a spermatic bulb is distinct from the prostate. GHISELIN (1966) considered this to represent an apomorphic state, largely on the basis of functional arguments. In some members of the Gastropteridae (GOSLINER, 1984; GOSLINER & ARMES, 1984) a spermatic bulb is present. However, in these species the bulb enters the penis by means of a separate duct, rather than emptying into the prostate, as in *Runcina*. Nevertheless, this structure is not found in any other cephalaspideans and is considered apomorphic.

**14. Penial papilla:** In most philinaceans, the penis bears a simple conical papilla, devoid of any elaboration or armature. In the aglajid genus *Melanochlamys*, some species bear a penial stylet or rows of penial spines (RUDMAN, 1974; GOSLINER, in press). These are considered to represent apomorphic states. In *Gastropteron pacificum* Bergh, 1893 (MACFARLAND, 1966; GOSLINER, 1984) there is a row of chitinous processes along the distal margin of the penis. Similarly, in *Siphopteron flavobrunneum* (Gosliner, 1984) there is a chitinous, subapical penial disc. In *Enopteron flavum* Minichev, 1967, a penial papilla is entirely wanting. These three states are considered to represent independently evolved apomorphies within the Gastropteridae.

**15. Penial duct:** In most members of *Siphopteron*, a narrow duct connects the anterior end of the prostate to the penial papilla. In the majority of gastropterids and other philinaceans the penial papilla is situated immediately anterior to the prostate, and no separate duct is present. The presence of an additional duct is considered to be apomorphic within the Gastropteridae.

**16. Penial bulb:** In species of *Siphopteron* that have developed a separate penial duct, there is a muscular area immediately anterior to the prostate. This muscular bulb, in turn, joins the penial papilla near the male aperture. This structure is not found in any other philinaceans and is considered apomorphic within the gastropterids.

**17. Penial bulb spines:** In *Siphopteron pohnpei*, *S. citrinum*, and *S. brunneomarginatum*, the penial bulb contains no rows of chitinous hooks. Within the penial bulb of most other members of the genus, are 2–4 rows of chitinous hooks. In some cases, the spines are arranged in longitudinal rows, whereas in other species there is a series of transverse rows. These two conditions are considered to



be independently derived. Both configurations are found in no other philinacean and are considered apomorphic within the Gastropteridae.

**18. Large penial spines:** In addition to possessing longitudinal rows of chitinous spines within the penial bulb, *Siphopteron quadrispinosum* has four large spines situated at the base of the bulb. This is considered a further modification of the penis within the family.

**19. Swimming:** The overwhelming majority of gastropterids are capable of swimming for long periods of time by flapping their parapodia. This is an autapomorphy for the family. However, several species have never been observed swimming and are unlikely to be capable of doing so. In these species, loss of swimming ability is considered apomorphic, because they are derived in virtually all other aspects of their morphology.

**20. Notched foot:** In species of *Sagaminopteron*, the anterior end of the foot is medially divided. This occurs in no other cephalaspideans and appears to be apomorphic within the Gastropteridae.

**21. Color:** Because most opisthobranchs are toxic, cryptic coloration is assumed to have preceded aposematic coloration (GOSLINER & BEHRENS, 1989). Virtually all primitive members of the Philinacea are inconspicuously colored and blend in with their substrate. A few species of *Philine*, which are epifaunal, are brightly colored and appear to exhibit aposematic coloration (GOSLINER, 1988a). Many, if not most, species of aglajids are brightly colored and exhibit warning coloration (GOSLINER, 1980; GOSLINER & BEHRENS, 1989). Some members of *Gastropteron*, such as *G. pacificum*, blend in well with a generalized substrate. Most members of the genus are brightly colored and probably exhibit aposematic coloration. The same situation occurs in *Siphopteron*, where *S. pohnpei* blends in well with its environment and all other members of the genus are brilliantly colored. *Siphopteron citrinum*, *S. brunneo-marginatum*, *S. michaeli*, *S. flavum*, *S. tigrinum*, and *S. nigromarginatum* all are yellowish or orange with brown or black pigment. This color pattern appears to be a derived feature uniting these taxa.

Species of *Sagaminopteron* are either brightly colored or bear special resemblance to their sponge prey. In this case, both are considered to represent derivations from a more generalized, cryptic color pattern.

**22. Pigmented parapodial margin:** In several members of the Gastropteridae, the margins of the parapodia strikingly contrast with the remainder of the body color. This is considered to represent a derived feature, which has arisen independently within different lineages of gastropterids.

**23. Pigmented siphon:** In species of gastropterids, the siphon, like the parapodial margin, may be of a contrasting color with respect to the rest of the body. Because the

coloration of the siphon is poorly correlated with the development of pigment on the parapodial margin, they are treated as distinct characters.

**24. Prostate gland:** Within the Philinacea, virtually all species possess a simple, short prostate gland at the posterior end of the cephalic penis. In some taxa, such as *Gastropteron rubrum* and *G. pacificum*, the prostate is elongate and highly convoluted. This is a modification of the plesiomorphic condition.

#### Phylogeny of the Gastropteridae

Having hypothesized the polarity of these characters, many phylogenetic analyses were performed using Phylogenetic Analysis Using Parsimony (PAUP). The data to construct phylogenetic analysis are provided in Tables 2 and 3. Many of the examined characters have multiple derived character states. In virtually every case, these are considered as unordered characters. This assumes that the sequence of change of the various derived states from the ancestral condition is unknown. However, in the case of the parapodial spheres, stalked spheres are assumed to be derived from sessile ones. Similarly, reduced jaw plates are assumed to be intermediate between ancestrally well-developed jaws and more-derived jaws that entirely lack plates.

These analyses produced an array of different most-parsimonious trees, depending on the combination of characters and taxa included, and the ordering of characters. The likelihood of these trees reflecting the true phylogeny of the Gastropteridae was then ascertained. A tree may be parsimonious in that it requires a minimum number of character transformation steps, but is not parsimonious from a functional point of view. For example, one family of trees required the evolution of a spermatic bulb from the hypothetical ancestor to *Gastropteron vespertilium*, its loss in other species of *Gastropteron*, its subsequent re-evolution in two species of *Siphopteron* and, finally, its loss again in other members of the genus. Complex characters such as the spermatic bulb are unlikely to undergo such multiple gains and reversals. A more parsimonious scenario for that character involves the development of a spermatic bulb in two independent lineages, once within *G. vespertilium* and again in *S. alboaurantium* and *S. flavobrunneum*. Other trees required the reduction of numbers of outer lateral teeth, their subsequent increase, followed by another decrease. Once radular teeth are lost in opisthobranchs, there is no evidence that they can be increased again in more apomorphic lineages. These scenarios also require the evolution of penial bulb spines, their loss, and re-evolution. These suggested character transformations may require fewer evolutionary steps, but are not parsimonious with what we know about character evolution within opisthobranchs.

Based upon phylogenetic analysis using PAUP and subsequent scrutiny of the required transformations, the fol-

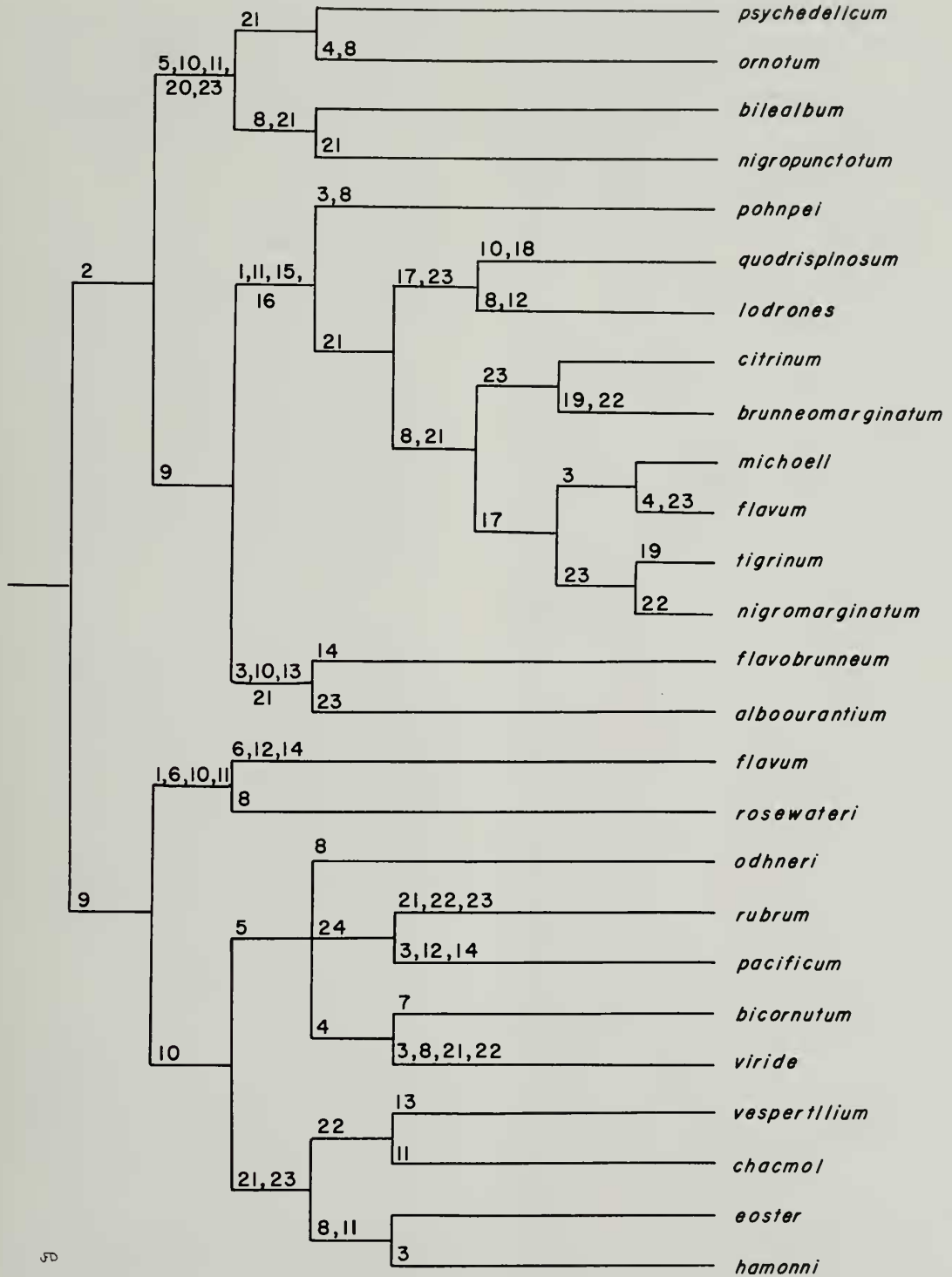


Figure 32

Phylogenetic relationships of the Gastropteridae.

lowing phylogenetic tree was produced (Figure 32). It requires 76 steps, three more than the most parsimonious tree produced using the same characters and taxa with PAUP. However, it is considered preferable because it reduces reversal and emphasizes the monophyly of some structures such as the prominent siphonal crest and complex penial structures. Other characters, such as reduction of the number of rows of radular teeth and the loss of the flagellum, are far more likely to occur many times within and between lineages.

#### Generic Divisions within the Gastropteridae

Previously, three genera of Gastropteridae have been described, *Gastropteron* Meckel in Kosse, 1813, *Sagaminopteron* Tokioka & Baba, 1964, and *Enotepteron* Minichev, 1967. *Sagaminopteron* was erected to accommodate *S. ornatum*, with two prominent denticles on the inner lateral teeth and a large number of outer lateral teeth. The addition of *S. nigropunctatum* Carlson & Hoff, 1973, *S. bilealbum* Carlson & Hoff, 1973, and *S. psychedelicum* Carlson & Hoff, 1974, confirms these attributes for the genus, though a large number of outer laterals appears to be plesiomorphic. Members of the genus have additional synapomorphies. Together with species of *Siphopteron*, members of *Sagaminopteron* have a prominent medial siphonal crest. Species of *Sagaminopteron* also have an elaborated gill with distinct pinnations on each pinna, appressed cerebral ganglia, and a notched anterior border of the foot. Plesiomorphic features include a well-calcified shell, a flagellum on the right side of the body, distinct subintestinal and visceral ganglia, and a simple penis.

*Enotepteron* was described to include the monotypic species *E. flavum* Minichev, 1967. It was distinguished by having a pair of stalked spheres on the posterior end of the parapodia, inner lateral teeth with a few, large denticles, and a lack of a penial papilla. With the addition of *E. rosewateri* Gosliner, 1988, the presence of spheres on the parapodia and large denticles on the inner lateral teeth characterize the genus. Other apomorphies include an absence of a shell and appressed cerebral ganglia. Plesiomorphic features include a siphon without a medial crest, simple flagellum and gill, and a simple penis, with or without a papilla.

All other species were included in *Gastropteron* (TOKIOKA & BABA, 1964; BABA & TOKIOKA, 1965; CARLSON & HOFF, 1974; HOFF & CARLSON, 1983; GOSLINER, 1984; GOSLINER & ARMES, 1984; GOSLINER, 1988a; GOSLINER & WILLIAMS, 1988), largely because they have fewer lateral teeth than in *Sagaminopteron*. What has become apparent is that there is considerably more morphological variability in these taxa than previously known. From the cladogram (Figure 32), it is apparent that several of these taxa form a monophyletic unit, distinct from *Gastropteron*. In each of the approximately 50 phylogenetic analyses that were conducted using PAUP, these taxa always formed a natural group. They are united by several apomorphic

features, including a reduced number of outer lateral teeth and a modified penis that contains either a spermatic bulb or penial bulb, with or without spines. Together with members of *Sagaminopteron*, they have a prominent medial crest on the siphon. On the basis of these apomorphies, these taxa can be clearly distinguished from species of *Gastropteron*, and are, therefore, placed in the new genus *Siphopteron*. The fact that members of this genus and *Sagaminopteron* have a prominent siphonal crest suggests that these two genera are more closely allied to each other than to *Gastropteron* and *Enotepteron*.

Once species of *Siphopteron* are removed from *Gastropteron*, it is necessary to determine what apomorphic features unite the remaining members of the genus. One feature stands out. All species have a prominent triangular extension on the inner margin of the inner lateral teeth. Plesiomorphic features include a shell, lack of a siphonal crest (together with species of *Enotepteron*), lack of a penial duct or penial bulb, and a truncate anterior end of the foot.

Based on this division of the family, the constituent members of the family are included in the following genera. Type species are indicated by an asterisk (\*):

#### *Gastropteron* Meckel in Kosse, 1813

- \**Gastropteron rubrum* (Rafinesque, 1814)
- Gastropteron bicornutum* Baba & Tokioka, 1965
- Gastropteron chacmol* Gosliner, sp. nov.
- Gastropteron hamanni* Gosliner, sp. nov.
- Gastropteron japonicum* Tokioka & Baba, 1964
- Gastropteron odhneri* Gosliner, sp. nov.
- Gastropteron pacificum* Bergh, 1893
- Gastropteron sibogae* Bergh, 1905
- Gastropteron vespertilium* Gosliner & Armes, 1984
- Gastropteron viride* Tokioka & Baba, 1964

#### *Enotepteron* Minichev, 1967

- \**Enotepteron flavum* Minichev, 1967
- Enotepteron rosewateri* Gosliner, 1988

#### *Sagaminopteron* Tokioka & Baba, 1964

- \**Sagaminopteron ornatum* Tokioka & Baba, 1964
- Sagaminopteron bilealbum* Carlson & Hoff, 1973
- Sagaminopteron nigropunctatum* Carlson & Hoff, 1973
- Sagaminopteron psychedelicum* Carlson & Hoff, 1974

#### *Siphopteron* gen. nov.

- \**Siphopteron tigrinum* Gosliner, sp. nov.
- Siphopteron alboaurantium* (Gosliner, 1984) comb. nov.
- Siphopteron brunneomarginatum* (Carlson & Hoff, 1974) comb. nov.
- Siphopteron citrinum* (Carlson & Hoff, 1974) comb. nov.
- Siphopteron flavobrunneum* (Gosliner, 1984) comb. nov.
- Siphopteron flavum* (Tokioka & Baba, 1964) comb. nov.
- Siphopteron fuscum* (Baba & Tokioka, 1965) comb. nov.
- Siphopteron ladrone* (Carlson & Hoff, 1974) comb. nov.



*Siphopteron michaeli* (Gosliner & Williams, 1988) comb. nov.

*Siphopteron nigromarginatum* Gosliner, sp. nov.

*Siphopteron pohnpei* (Hoff & Carlson, 1983) comb. nov.

*Siphopteron quadrispinosum* Gosliner, sp. nov.

#### *Incertae sedis*

*Gastropteron sinense* A. Adams, 1861.

### Taxonomy of Species of Gastropteridae

The above arrangement of species within gastropterid genera is somewhat tentative, owing to the incomplete description of several taxa. *Gastropteron japonicum* Tokioka & Baba, 1964, is clearly placed within *Gastropteron*, based on its external and radular morphology. However, TOKIOKA & BABA (1964) noted its similarity to *G. pacificum*, and stated that it differs in having fewer (13) gill pinnae than *G. pacificum* (16–20). Because the penial morphology of the former remains undescribed, the separation of the two species remains tentative. *Gastropteron sibogae* Bergh, 1905, is incompletely described and its penial morphology remains unknown. However, it appears to be distinct from other members of the genus, as it lacks denticles on the inner lateral teeth. *Gastropteron viride* Tokioka & Baba, 1964, has a gill similar in shape to that of *G. rubrum*, *G. pacificum*, *G. japonicum*, *G. bicornutum*, and *G. odhneri*, but differs from all of these in having modified inner and outer lateral teeth and in having a terminal knob on the posterior of the visceral hump, as in *Siphopteron flavum*. The penial morphology of *G. viride* remains unknown.

The internal morphology of *Siphopteron fuscum* Baba & Tokioka, 1965, remains unknown. However, its distinctive color pattern ensures that it is separable from all known members of the family. It is placed within *Siphopteron* because of its small body size, prominent siphonal crest, and reduced ctenidium.

### Biogeography of the Gastropteridae

Within the family Gastropteridae, the genus *Gastropteron* is the most widespread with both temperate and tropical taxa in all the world's oceans. *Gastropteron rubrum* is known from the Mediterranean and West Africa (not from the western Atlantic, see discussion of *G. chaemol*). Two species, *G. vespertilium* and *G. chaemol*, are known from the western Atlantic. *Gastropteron pacificum* is known from Alaska to the Gulf of California and possibly Japan, if it is conspecific with *G. japonicum*. The tropical Indo-Pacific species *G. bicornutum* is known from Japan and Papua New Guinea. The remaining species are known only from their type localities.

Members of *Enotopteron* and *Sagaminopteron* are known from the Indo-Pacific tropics, with the exception of *E. flavum*, which is subtropical in the Indo-Pacific. *Sagaminopteron ornatum* is known from Japan and Australia (Richard Willan, pers. comm.) and *S. psychedelicum* is

known from the Marianas Islands, Papua New Guinea, and Reunion Island. The remaining species are known only from the type localities.

Virtually all species of *Siphopteron* are known only from the Indo-Pacific tropics, the exceptions being *S. alboaurantium* and *S. flavobrunneum*, which are known only from the Atlantic coast of the Cape of Good Hope Peninsula, South Africa. It should be noted that many endemic southern African species have historical biogeographical links with the Indo-Pacific tropics (GOSLINER, 1987). The phylogenetic analysis provided here would also suggest that this is indeed the case for these taxa. Several members of this genus are widespread. For example, *S. ladrones* is known from Aldabra, in the western Indian Ocean and Guam, and *S. tigrinum* is known from Palau, New Guinea, Australia, and Madagascar. Several other species are widespread in the Pacific Ocean, but have not been found in the Indian Ocean. *Siphopteron quadrispinosum* is known from Papua New Guinea and Hawaii and *S. pohnpei* is known from Ponape and Hawaii. *Siphopteron flavum* and *S. brunneomarginatum* are widespread in the western Pacific Ocean. The remaining species are known only from their original description.

Most of the evolution within the Gastropteridae has apparently occurred within the Indo-Pacific tropics.

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